AMERICAN FOSSIL CYCADS

VOLUME II

TAXONOMY

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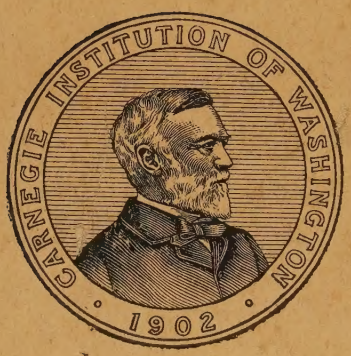
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, Washington 98112

BY

G. R. WIELAND



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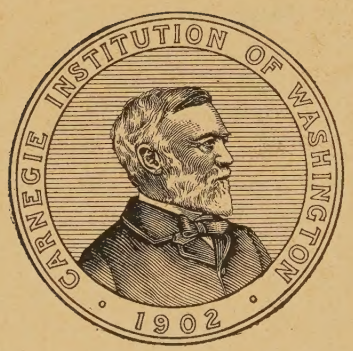

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PREFATORY NOTE.

In bringing to completion a second volume on the petrified cycads the material inviting exact study seems more impressive than ever. The actual number of stems in the several collections has not been much increased since the publication of Volume I, but the aggregate of finely conserved structure which is gradually being located and made available for study is great. Nor do the European collections fall behind those of America in interest. Although somewhat less extensive, their structural interest coequals that of the American collections.

Easily the most noteworthy addition to the American series is the monocarpic trunk of the United States National Museum discovered by Dr. N. H. Darton in the Hermosa segment of the Black Hills Rim—in certain respects the most remarkable fossil plant of any kind or age ever recovered. Fortunately, however, the study of the Cycadeoids has reached a point where progress is less dependent on rare or unusually conserved specimens. To this result the discovery of related Williamsonians has greatly contributed; equally so the precise methods for the study of casts and imprints introduced by Professor Nathorst and others. The expanding field of cycad investigation has thus taken on permanent interest, and it is certain that museum collections will be signally enlarged, while those already accumulated hold the attention of botanists.

In the prefatory note to Volume I the opportunity for extended study and comparison of Cycadeoidean seeds was emphasized, and it is believed that the chapter now devoted to this subject fully justifies singling it out. Even without the increase of material afforded by the Hermosa cycadeoid it was evident that the seeds held far greater interest than the space earlier devoted to them indicated. At the present time, amongst subjects near at hand, the simpler one of stem structure may be noted. The anatomy of the fossil gymnosperms has long been an unsatisfactory subject because of the great size or fragmentary character of the Mesozoic stems. The wedge of a *Cycadeoidea* trunk is comparable to the wedge of even the tallest conifer. It affords complete structural details within restricted limits and later studies will reveal the type of change which may be expected in gymnospermous stems in passing from pith to cortex and from base to apex.

The unexpected discovery of the horned disks of *Cycadeoidea colossalis* has led to comparisons with seed-coats suggesting some kind of ancient and far-reaching homology between megaspore and floral envelopes. The ideas advanced are not theories; they are hypothetic. If any of these conceptions should later receive confirmation or proof their importance in evolutionary theory must be very great. For this reason the discussions of the closing chapters take on a speculative form. No claim of triumphant demonstration is made or under the circumstances can be made. Refutation there may well be. But in either instance it is with confidence that the group origins are held to be more nearly discrete than may be implied from most discussions of the theory of descent.

It has been found necessary to lay increasing stress on the need for adhering to the nomenclature of convenience already established for the silicified stems. This is indispensable to progress in the taxonomy, and to a certain extent in general structure. These stems are unique, and must be recognized as difficult to catalogue.

Both in the pursuit of the general subject of cycad investigation, and in the preparation of this volume a number of associates and others have aided wherever opportunity offered,

either through direct courtesy or in zealous collaboration. To the kindness of Dr. N. H. Darton, of the United States Geological Survey, is owed the fine photographs of Black Hills Rim structure showing *Cycadeoidea* terranes, facing Chapters II, V, and VI. Professor G. F. Kay, of the State University of Iowa, has contributed the photographs of Figure 1 and Plate XIII, showing the Macbride collection. The photographs of polished Cycadellas facing Chapter VIII are by Professor R. S. Bassler, of the United States National Museum. Dr. Marie C. Stopes, of University College, London, furnished the photograph of the remarkable branched Japanese *Cycas* (Fig. 7). Mr. G. W. Grabham, of the British Survey, Khartoum, forwarded the photograph of the Lado cycad on which is based Figure 96. To Professor H. H. W. Pearson, of the South African College, Cape Town, is due the series of photographs given in Chapter XIII showing the habitus of South African cycads. The photographs of Oaxacan Williamsonias illustrating Chapter XII are by F. de P. Carbajal, of the City of Mexico. The photograph of the pure stand *Araucaria* forest (Fig. 94), is contributed by Sr. Estéban C. Ferrari, of Buenos Aires.

Mr. G. S. Barkentin, whose pen added so much to the illustration of Volume I, has also made the principal line drawings for Volume II; several others are by Miss Lisbeth Krause, and the original figures of *Williamsonia*, which are a feature of Chapter XII, are by Mr. R. Weber. Mr. Fred W. Darby, of the Yale Museum, has drilled out cylindrical cores from various types and other trunks and has made the chief series of sections on which Volume II is based. The large size of most of these sections renders them difficult to cut, but adds greatly to the interest of the plates. Some lesser sections are by W. Harold Tomlinson, of Swarthmore, Pennsylvania. The comparisons with Carboniferous seeds of the English "coal balls" have been verified from purchased material cut by the well-known English sectors, W. Hemingway and James Lomax.

Dr. F. H. Knowlton, of the United States National Museum, has aided with valued suggestions and material. The curator of the United States National Museum, Dr. George P. Merrill, has had sawn various Cycadeoid types, as well as other specimens. The trunks cut include certain Yale specimens from the Black Hills and also others from the Isle of Portland, affording comparative data never before available. The finest of these latter were generously donated to Yale by the Bath Stone Firms, Ltd. This extensive elaboration of new material will, however, aid mainly in future studies. Fully accepting the responsibility attaching to the conservation of the great collections in the Yale University Museum, the curators have at all times shared most generously in funds devoted to paleontologic research. To Professors Charles Schuchert, Alexander W. Evans, and Alexander Petrunkevitch, of Yale, hearty appreciation is extended for sharing facilities and help.

When the hard-won results of the students of other days, the tedious processes of earlier book-making, and especially the difficulties involved in securing adequate illustration are considered, the writer esteems himself peculiarly fortunate in having had the aid and advice of the officials of the Carnegie Institution of Washington in bringing this supplementary volume to successful publication.

G. R. Wieland.

Yale University, New Haven, Connecticut.

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AMERICAN FOSSIL CYCADS

VOLUME II—TAXONOMY

By G. R. WIELAND

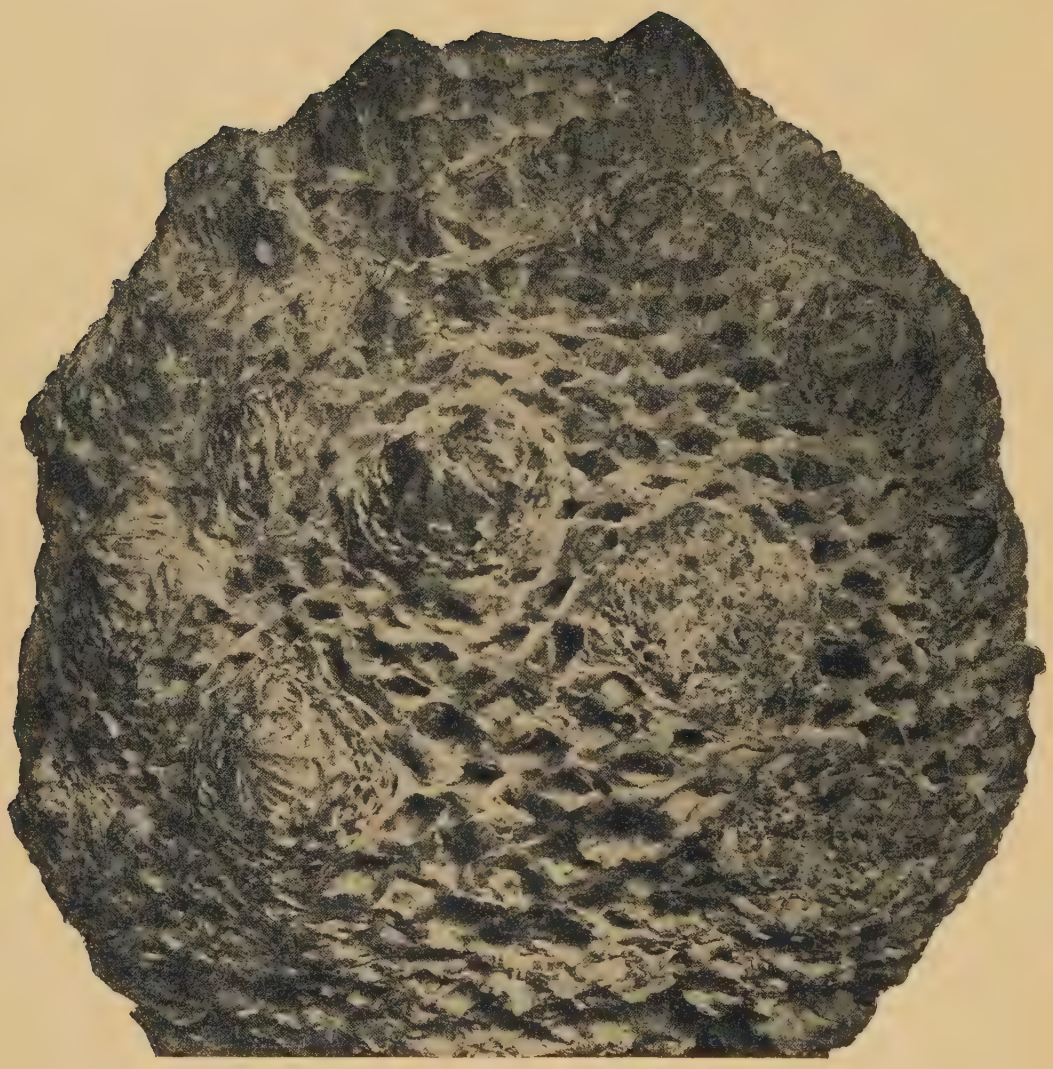


FIG. 1.—*Cycadeoidea* (Bennettites) *dacotensis* Macbride. Lower Lakota formation of Darton. From photograph by Kay. About one-third natural size.

This was the first of the Black Hills Cycadeoids to receive scientific description. It is now in the museum of the State University of Iowa. It was collected at the famous Minnekahta locality of the southern Black Hills rim by Professor Thomas H. Macbride during the summer of 1893. Like the great *Cycadeoidea Reichenbachiana* of the Zwinger Museum of Dresden, this remarkably conserved silicified trunk, fairly ranking among the five or six handsomest ever discovered, remains unstudied, its conservators having objected to sectioning. The large size of the flower-buds, equaling that of smaller vegetative branches, is a notably interesting transition feature.

CHAPTER I.

STATUS AND SCOPE OF FOSSIL CYCAD STUDY.

When these investigations of fossil cycads were begun, sixteen years ago, the broader field of study appeared to divide itself into three or four parts, each meriting treatment in memoir form. In the first place, it was clear enough that, following the preliminary cataloguing by Lester F. Ward, necessarily based on salient features, the most urgent need was to further illustrate macroscopic details and at the same time to go sufficiently into the histologic structures to bring out clearly the main vegetative and reproductive characters of the Cycadeoideans. The extensive and rapidly accumulated American collections had not only made this simpler study possible, but necessary, if the many new facts of Cycadeoidean structure so clearly illustrated were to be brought into the fund of general botanic knowledge within reasonable time; for any attempt to deal with species from the very beginning of study would have long delayed the appearance of many interesting facts, clear enough in themselves.

Secondly, it seemed the most feasible plan to follow up the initial study of structure with the taxonomy of the fossil cycads—an immense task, since obviously enough the only sound basis of a completed taxonomy is ultimate histologic detail.

Thirdly, it became highly desirable to begin field study in the mid-Mesozoic strata yielding Cycadean casts and imprints. The results of previous collection had been little satisfactory, and there was the liveliest hope of increasing the slender amount of known material, while the application of the new-found knowledge of the cycads gained from the fortuitous conservation of a single isolated group of specialized robust forms promised to unravel the development and history of the Cycadophytans, especially the so-called Williamsonians of the Trias and Lias. Undeniably the perfection of the American silicified Cycadeoids has given a great impulse to the study of Cycadophytans in general. It is hardly forgettable that in all the course of collecting, from the days of Williamson and Brongniart down to the present time, the only Yorkshire Coast Williamsonian stem found with mature leaves attached is the historic specimen of the James Yates collection in the Paris Museum; only after the demonstration of numerous crowns of young leaves in the Black Hills specimens was closer attention turned to certain Indian cycad trunks bearing basal portions of *Ptilophyllum* fronds, and the Skone *Wielandiella* completes the list.

Similarly, when the true nature of the Williamsonian fruits and their virtual identity with those of *Cycadeoidea* had been learned from the study of the latter, it became apparent that the gymnospermous facies must be an exceedingly varied one. Evidently the small group of *Williamsonia* fruits obtained by the earlier collectors on the Yorkshire coast foreshadowed the discovery of allied series in many of the horizons yielding cycad fronds. In fact, if any further zest to study afield was required, it was assuredly given by the increasing possibility that locked in the recesses of the complex of proangiosperms, as Saporta had boldly called the Williamsonias, there must be found many suggestions of the mode of origin of the angiosperms. The ancestors, or at least the pseudo-ancestors, of these, it seemed, might actually be found amongst the Cycadophytans which so evidently domi-

nated the early Mesozoic forests of the globe. The "sudden emergence" of the angiosperms from the hidden depths of these forests seemed, so far as the fossil record went, an even more impressive fact than was once supposed. Furthermore, it soon became very clear that each new set of facts gained from the study of imprints and casts must help in the study of the silicified series. Just as the latter had aided in clearing up the Williamsonian riddle, so all more ultimate conceptions of the silicified series depend on the study of the much more varied related forms; and these even afford comparative histologic data. The accurate methods developed by Nathorst and by Hollick and Jeffrey for studying partly carbonized imprints and casts now frequently yield results falling but little short of those gained from the finer silicified and calcified stems.

Finally, as a somewhat tentative fourth line of effort belonging within the field of present-day botany, a far closer study of the structure, ecology, and species of the existing cycads thrust itself forward as another equally great desideratum. In fact, the general study of existing cycads has kept pace with rather than anticipated investigation of the fossil forms.

The lines of study outlined in the foregoing paragraphs were of course held subject to reasonable modification; and indeed conceptions of the field involved and of the possibilities of accomplishment in it have led to changes of both method and order. In particular, following the preparation of Volume I, it was presently found that it would be much more difficult to bring out a completed taxonomy of the American Cycadeoideæ than was at first anticipated. The great number of specimens which might reasonably be studied need not be cited; neither is it necessary to mention the more thoroughgoing examination of arbitrarily named foreign material from both England and Italy which is well represented in the Yale University and National Museum collections. But the lack of facilities for cutting longitudinal and transverse sections of important types and cotypes proved severe and it soon became evident that taxonomic data of absolute value could not be so rapidly accumulated. Then, too, the magnificence of the material led to the attempt to cut thin sections of a large and striking size—seemingly indispensable to the study of the particular specimen in hand, but most difficult to make and thus fatal to the accumulation of that more extensive series of sections needed to complete the descriptions of histologic detail and to identify with certainty a long list of species.

As it turned out, the cycad studies early broadened almost to the limit of the resources at hand and a time was soon reached when it became a pertinent question whether the interests of pure science might not be more effectively advanced by field studies of the Mexican Mesozoic. It was learned through Señor Aguilera, the director of the Geological Institute of Mexico, that cycad fronds occurred in some abundance at several points in the Mesozoic strata of the States of Puebla and Oaxaca, though such had never been studied or described But this was by no means a wholly new venture; a reconnaissance of some of the Mexican country, for the double purpose of studying existing cycads and searching for possible fossil forms, had already been mentioned when plans for cycad research received their first tentative outlines. Then the only southwestern occurrences of Mesozoic Cycadophytans noted in the literature were the few Triassic fronds described by Newberry (205) in the record of the San Juan expedition and a single Pueblan form later named by Ward in the eighth report of the U. S. Geological Survey, without figures, and now lost to view.

It was thus with deep interest that arrangements were discussed with Señor Aguilera, looking forward to a temporary transfer of the course of cycad work to the Mexican field;

and, these changes being sanctioned by the officials of the Carnegie Institution of Washington, with great liberality, fossil cycad study in Mexico was finally begun and carried on during 1909 and 1910. This work, including some minor collecting in Sonora, which was not followed to a conclusion, was confined mainly to the collection and description of a fine fossil flora secured during the early part of 1910 in western Oaxaca, in strata found to be of lowermost Liassic age. In general, the lower Liassic series of plants, brought together from quarries fairly representing a carefully measured section 2,000 feet in thickness, proved unexpectedly rich in Cycadophytans—the material equaling, if not exceeding, that from the Yorkshire coast and Indian regions in variety of forms and conservation, and indicating almost unlimited possibilities of further collection.

Thus, these new and rich collections of plants, adding so much of stratigraphic interest in denoting the first typical Liassic series from the horizons of the Western world, were discovered and studied most opportunely; for they have increased materially our knowledge of the group to which the Cycadeoideæ belong, and furthermore, the direct study of the silicified specimens has been made far more luminous and facile by this actual contact with more varied stem, foliage, and floral types. Just as in Triassic and Jurassic time, Mexico still remains a great cycad center and it is often possible to collect both existing and extinct forms from neighboring hillsides or even on the same areas.

At the same time that field work was begun in Mexico, Professor Nathorst, who began his singularly interesting studies of fossil cycads with the collection of *Williamsonia Leckenbyi* at Clougton Wyke in 1879, made the first of a series of incursions into the rich Jurassic cycad terranes of the Yorkshire coast; his discovery of the staminate flowers of *Williamsonia* was made simultaneously with my own finding of a typical example of somewhat different species in Oaxaca; a little later Professor Chamberlain began an active study of the existing cycads of the world, while Professor Thomson carried out his study of Araucarian stem structures. Miss Bancroft published a highly interesting study of the petrified cycads of India with leaves attached, and Professor Seward has given a careful study of the fine Williamsonian ovulate strobilus from Scotland, long since figured by Hugh Miller in the "Testimony of the Rocks." Meanwhile, Professor Lignier has carried forward his interest in the Cycadeoideæ, Capellini has given some further notice to the Italian cycads, and other papers of more or less direct interest have appeared. In view of all this progress it has seemed that any delay in the study of the silicified series, occasioned by the taking up of Mexican work, has been more than justified.

Thus all four of the lines of study first suggesting themselves have been followed by the writer directly or by others. The study of structures, taxonomy, and distribution has been pushed forward with but little variation from the original plan. If time has been diverted from the study of the taxonomy, so that this subject can not at once be treated as completely as was at first hoped, the study of the superb Mexican Liassic Cycadophytan series has in no small measure compensated for this. Unquestionably the field of cycad study has been broadened, so that it is now certain that the student of the future will content himself with nothing short of a fossil cycad survey of the globe. While all this recent progress has served to make it clearer and clearer that the Cycadales form a group which, although fairly homogeneous in itself, presents a structural variety at first wholly unsuspected, an even larger result looms into view; for it now appears that the completer knowledge of the cycad complex is not merely requisite to a clear conception of Mesozoic plant life, but essential to an understanding of the final stages in the evolution of the higher types of seed plants.

What the future course of cycad study may be is perchance a little less certain now than it was ten years ago. The field has broadened so that it is not easy to declare which course of work is relatively the more urgent. Perhaps the discovery of related groups intermediate between cycads and conifers, or more cycad-like Cordaiteans than have been thus far detected, will again bring us to the stage of distinct and clearly recognized tasks; the field is the fountain-head of progress in paleobotany and of further advance in cycad study.

It would of course be unfair to the diligent students of many lands, who have often accepted negative results without complaint or regret, to say that any line of paleontologic field-work is lightly regarded. Yet field-workers themselves are in part responsible for a relatively slow development of the methods of plant collection. From consideration of available collections and modes of fossil-plant occurrence I am more and more led to insist on the paramount importance of field-work and the necessity of developing quarries on a large scale. Good fortune afield has changed all my earlier conceptions of the scarcity of fossil plants, whether found silicified, as casts, partly carbonized, or as imprints. In the case of imprints, by trenching at favored points rather than by mere dependence on isolated ledges or superficial quarries, it will be possible to secure plant series far more representative than those hitherto brought to light. It has long been my opinion that the Yorkshire coast, for instance, could not possibly have been exhausted of plant species or special forms of conservation of both foliage and fruits, "*ausgebeutet*," and this opinion has been more than justified by the recent discovery of abundant new material in readily accessible strata as reported by Hamshaw Thomas. Similarly, the experience gained on the great El Consuelo section, studied under the advantages of an unsurpassed climate and considerable leisure for observing the kind of results obtainable from trenches and quarries, led to the conviction that the plant species there secured could be doubled by systematic methods of collection and preparation. As elsewhere recorded, the Rio Consuelo plant-beds form a syncline which is cut through in its entirety on the Barranca Consuelo, so that opportunity is afforded for a double series of collections within the range of a few kilometers; and consideration of the other Jurassic series that have been obtained where there is a succession of plant-bearing strata leads to the same suspicion of incompleted collection.

Even more convincing have been the facts learned of the possibilities of silicified cycad collection. Indeed these are already demonstrated at the quarries of the Isle of Portland, where, however, there is no great number of finely petrified specimens, as at some of the localities in the Black Hills. Careful study of these latter, with the collection of some trunks found *in situ* and the gathering of data from all who had ever made collections in the "Rim" country, showed conclusively the relation, abundance, and position of material in the terranes. At Minnekahta it would be practicable, by means of a shallow quarry of some width, to secure an extraordinary wealth of material illustrating the extent and appearance of the cycad forest with a completeness such as no series of eroded out and often surface-worn trunks could possibly yield. The cost of such operations would be large, although scarcely a tithe of that devoted to quarrying for Dinosaurs in recent years; but the results must unfailingly prove both instructive and striking.

The conclusion, therefore, is that in the further study of Mesozoic plants, and of the cycads in particular, the primary need at present is renewed activity afield, which should extend to all known localities. In other words, it becomes necessary to regard field-work on the fossil cycads at least as seriously as students of fossil reptiles hold the study and collection of Dinosaurians. In reality, both these lines of paleontologic investigation are

essentially complementary; they serve to forge inseparable links in the great chain of paleontologic evidence.

We have already seen the study of plant evolution broadened out and set far forward by the discovery of the Sphenophyllales, the Cordaitales, the great types of the Carboniferous, and the seed ferns, and with each succeeding year expectation increases that other equally important bridging series may, as the result of exceptional finds or preservation, be successfully investigated. All the past history of paleobotany implies the discovery of other groups wholly unknown or but partly hypothesized. Among the latter may be instanced early Gnetaleans and Coniferales. Similarly, it is now clear that much will yet be learned of the early seed types, and it is becoming more evident that the supposedly small likelihood of the discovery of new types unheralded in the foliage record is not founded on fact. Within the past decade it has become more apparent that the present leaf-record still holds in store many surprises in stem and floral structures.

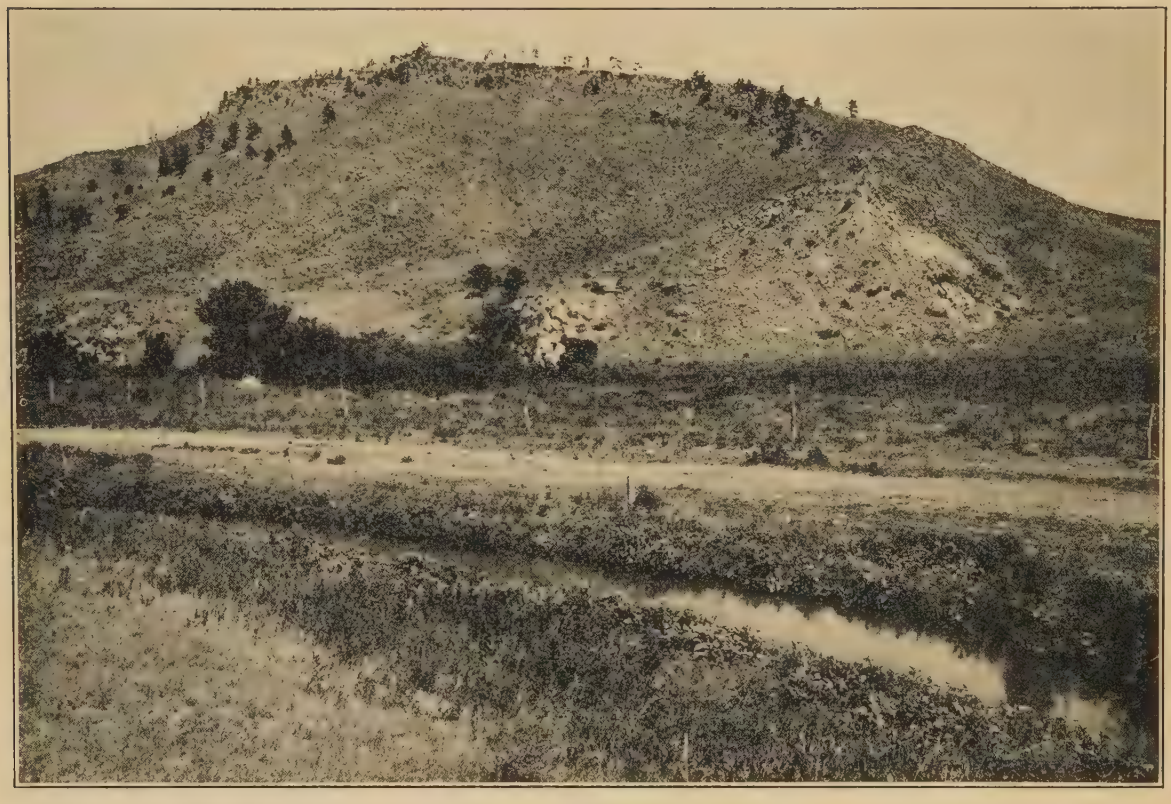


FIG. 1*a*.—Dakota-Lakota sandstone Rim of South Eastern Black Hills. North side of Buffalo Gap, South Dakota. Looking north. A typical water-gap through the "Rim."

The "Rim" consists in the more or less easily eroded rocks of the Trias and Marine Jura followed usually by the Morrison shale, Lakota, Minnewaste (local), Fuson, and Dakota formations. The Dakota sandstones form the main cap below which are pine dotted talus slopes of Fuson and Lakota to the left. These face the Permo-Triassic "Red Valley." Silicified logs are frequent along this inner slope. The Cycadeoids of the Lakota horizon occur more rarely. The lower or Morrison shale horizon is here absent. Compare with the views of the Cycad Valley, Plate XLIX, Volume I, and with Figures 8*a* and 14*a*. Photographed by N. H. Darton.

CHAPTER II.

CRITERIA OF CYCADEOIDEAN SPECIES.

Ordinarily it is relatively easy to distinguish those lesser differences in plants which are by common consent termed specific, and which must necessarily be observed and described, in order to make headway in the study of any considerable assemblage of fossil forms. In studying existing forms sections are soon cut where needed, while in assigning specific values to collections of fossil plants there is usually little doubt as to which are relatively uncertain and which absolute characters. In fact, those differences of usage, largely temperamental, which lead one worker to divide an assemblage of fossil leaves, fruits, or stems into many species and varieties, and another to "lump" his material, are always held in mind by all students of the fossil record, and in the end need occasion slight inconvenience. All workers understand that if on the one hand a proneness to create species produces a bulkier literature, on the other a failure to discern or define to the full extent the true specific distinctions in a given assemblage of fossil plants means labor unperformed, while no student willingly fails of either accuracy or balanced judgment in his specific determinations.

But how to best combine the qualities of industry and judgment in the following discussions of species has indeed proven something of a task. Where so many examples are present in a series of silicified cycads exhibiting every stage of growth from small trunks or branches which are the equivalent of young trunks up to plants bearing 400 or 500 strobili with mature seeds like the Darton cycad, it would at first seem that most specific data could be securely established and applied, as indeed they can be within certain limits. But these explanations are given for the double purpose of somewhat clearing our own views and conceptions of species, and at the same time bringing before the vision of students of plants, who may not have examined large assemblages of silicified cycads from different horizons and localities, some of the difficulties of specific or even generic determination here met with. In Chapter II, Volume I,* the peculiarities of preservation in silicified cycads have been fully discussed, so that it is unnecessary to go over that subject again. From the facts then brought out it should be clear enough that in outer appearance the several series of silicified cycads are very variable indeed, and that neither in form nor structure is there a fixed degree of constancy in trunks from a given locality. Those from the Isle of Portland are more difficult to assign to groups on the basis of macroscopic characters than any of the American series, though far from lacking in diagnostic features. Of the four American series of cycad trunks, clearness of outer characters is greatest in the Piedmont-Black Hawk trunk group, and next so in the Maryland trunks; while in the Minnekahta group of trunks with various freely branching specimens, and the Wyoming series with a very free growth of ramentum, in the great majority of cases it is about equally difficult to say from external characters just what specific form one may have in hand. When we consider the Piedmont-Black Hawk trunks (series shown on Plate 4) with as clearly defined outer characters as

*American Fossil Cycads (Structure), Carnegie Inst. Wash. Pub. No. 34, constitutes Volume I of the work here continued as Volume II (Taxonomy). At the time Volume I was published it was fully intended to take up the preparation of a second volume. But inasmuch as it was well understood that this would require a long period of preparation and that other phases of cycad investigation might meanwhile be attempted, a volume number was omitted. It is now given and will be used henceforth without further explanation.

any group in the world, not even excepting the fine series of Italian trunks in the Capellini Museum at Bologna, it will at once be evident how severe may be the limitations to accuracy in interpreting external features in a small group. Doubtless a form like *C. rhombica* may always be recognized by its small leaf bases with regularity of spirals and very scant ramentum; while it does not seem likely that a characteristic specimen of *C. superba* or *C. Stilwelli* would often be confused with other species. Yet one is not always sure of the modifications which might occur within the given series, and any of these species would certainly look very different if conserved under varying conditions as members of any other series—for instance, the Maryland group, where one can by no means assert they are not in actuality present under different names. And the difficulty is marked when the attempt is made to separate types like *C. ingens*, with enormous leaf bases and heavy ramentum, from the columnar type called *C. Jenneyana*, a species which has priority over the others; for there is so much of transition in general appearance of trunk armor and leaf bases that a majority of the trunks appear to fall into a series of border forms most difficult to place! Still more perplexing may become the problem of separating from *C. Jenneyana*, with its marked irregularity of leaf base, the cycad called *C. excelsa*, found at Minnekahta just 60 miles away. Thus far, the case is put at its simplest; but it soon gets complex, and if specific values so soon become uncertain in the very localities where trunk characters are most striking, it is readily understood that comparing species from widely separated localities always involves more or less uncertainty; nor is the problem made easier by the fact that there is not the slightest reason to doubt that the valid species of *Cycadeoidea*, taking the museums of the world over, are already as numerous as those of existing cycads.

However, if numerous transverse sections of the armor afford a fair means of control in judging outer characters, may not a further and surer set of specific indices be found in the gross development of wood zones of the Piedmont-Black Hawk series of cycads? Yes; but the trunks are excessively chalcedonized and difficult to cut; and with the exception of the U. S. National Museum equipment recently installed, where can be found the appliances for cutting and polishing the necessary series of transverse and longitudinal sections of these huge trunks, even if time sufficed to carry out such operations? In the case of the entire Piedmont-Black Hawk series, therefore, it is possible so far to observe only the longitudinal development of the wood-zones from fractured trunks, in but one instance affording a convenient longitudinal section scarcely complete enough to illustrate.

The polished transverse trunk sections are fortunately easier to prepare from trunk segments, and there are now available a half dozen of marked interest. As already recorded in Volume I, the heavier types of wood-zone development exceed anything previously known in cycad-like plants. Growth rings far stronger than those of *Dion* are present, and it is obvious that when the trunk sections are adequately extended it will be possible to firmly establish the identity of nearly all specimens. Furthermore, the presence of two generic types of wood development is quite possible, the one very light, the other heavy.

It follows that, for the time being, only the general features of the trunk sections can be illustrated. Plates 8 and 9 seem to indicate quite clearly that in the case of the two gigantic columnar forms, *C. ingens* and *C. Jenneyana*, there is a marked difference in the development of the woody cylinder; although as the great type *C. ingens* remains uncut, its medullar and wood development may only be fairly surmised from lesser specimens. On Plate 6 medium-sized trunks, with both light and heavy wood development, are illustrated; while Plate 43 offers very clear testimony as to the general nature of wood zones, especially with reference to the rate of decrease toward the summit. Yet, so long as we lack the

necessary series of longitudinal trunk sections required to show the actual wood development, not to mention the specific range in different trunks due to growth stages or other factors, specific values must remain uncertain. At present, therefore, we can only approximately tie up the series of trunk sections on the basis of the armor, woody cylinder, and medulla taken together, with any minor check which the ramentum, wood structure, or the presence of any young leaves may afford.

When we come to fructification, the subject of specific indices at times becomes even more complex. Indeed the means of final comparison in the given instance is nearly always lacking because of varying stages of growth or the outright difficulty of securing the needed sections. Yale trunk No. 115 of Plate 6, photograph 2, is an isolated case in which a monœcious condition is adjudged to be present; there can hardly be any doubt of this. In fact, very shortly after the complete evidence in the case of this trunk had been gotten together I had the pleasure of reviewing it with the eminent student of evolution and botany, Professor Hugo DeVries, who could see no reason why he should withhold his sanction for regarding the monœcious condition as definitely proven in this instance. But the axis of the aborted cone of the staminate flower-bud is elongate and the parenchymatous cushion of the well-grown ovulate cone is short and globular; whence, as no other of the limited number of Black Hawk trunks shows the short cushion or permits certain judgment as to the functioning of its flowers, these ordinarily crucial characters can only be used in remoter comparison with certain Minnekahta trunks. Such, in brief outline, are some of the difficulties encountered in assigning specific position to the Black Hawk cycads. Yet it is no more than fair to say that the species are in general assigned within the limits of reasonable accuracy and that the results presented here will doubtless be found sufficiently definite for all practical purposes.

When we turn to the great Minnekahta series of trunks, slightly different difficulties arise. Preservation is far better, and a considerable number of the trunks have very well-marked fruits, while the unique branching trunks are exemplified by some strikingly complete specimens easily ranking among the handsomest fossil plants ever recovered. But the large number of broken or isolated or worn branches makes it even more difficult to assign species on the basis of outer characters, and the mass of material for comparison is simply overawing. As a result we can by no means have so full a degree of confidence in the specific determinations of this great series as would be at first anticipated.

In taking up the Carbon County (Wyoming) trunks called *Cycadella*, there is still less of certainty, it being necessary to treat this series in a purely tentative manner; for owing to the presence of much ramentum and the crushed condition of the trunks, notwithstanding excellent silicification, it would be necessary to make both trunk and lesser sections in the case of nearly every specimen in order to even approximately determine its true specific position.

Similarly in the case of the Maryland cycads little more than a critical review of previous work can be given. Originally referred to a single species, these trunks were subsequently referred to a half dozen separate species on grounds which, as will later be pointed out, hardly seem defensible. Nevertheless, in the case of this or any other series of trunks, large or small, a lingering doubt must always remain so long as the crucial sections remain uncut. It is not too much to say that trunks belonging to widely separated genera might outwardly simulate each other in every respect.

Between the silicified cycads and the leaf and fruit imprints are certain intermediate types of conservation consisting in semi-mineralized armor casts, of which no American forms have so far been reported; but a small and interesting series of such types has been

described by Fliche (1891) from the Albian-Cenomanian of the Argonne. The mature fruits of *Amphibennettites Renaulti* have seeds over 1 cm. in length, these being the largest known in the Cycadeoideæ. It would be interesting to know more about such recent members of the group. Of the validity of the several Argonne species little doubt exists, although only a slender group of characters is present. Finally, there are the carbonized forms, with structure, and the structureless casts of the Mexican Liassic and elsewhere.

It is thus seen that, great as are the difficulties met in determining the silicified trunks, they are not as yet much increased by uncertainties due to intermediate types of preservation. The silicified groups may, in the course of time, be found to include types closely approaching the less conspicuous casts, and these may in turn grade into ordinary imprints. But the time of really varied and extensive collections is still remote, and aside from the difficulties just outlined, the only further points of uncertainty in the determination of the silicified trunks of America arise from questions of priority in the case of the Isle of Portland, Italian, and other European cycads. These latter points are, however, of merely minor significance here, partly because real differences can be cited in most instances, and also because it is usually a fair assumption that the European specimens are of distinct species. That this is so has, for instance, proven true of the isolated cases where close comparison of the seeds has been possible, the seed structures plainly showing specific variation. If we could make a truly critical comparison of all the American and European forms, there is little doubt that there would be some overlapping of species; doubtless in the course of a few years more of histologic study a distinct species overlap will begin to appear. As will later be made evident in the present memoir, the European and American Cycadeoideæ are so alike that it is reasonably sure they were all derived from some common center of dispersion or are the result of some single evolutionary movement or impulse.

Having shown what the chief difficulties encountered in assigning cycad trunk species arise from, it is now in order to very briefly review the specific indices on which a due reliance can be placed.

In Volume I, Chapters II and IV, the types of trunk preservation, the differences in appearance due to crushing or compression at varying angles to the stem axis, and especially the armor variation due to erosion or the extent of armor preservation, as well as the varying appearance of armor sections cut at different levels, together with those disturbances of the armor-pattern due to the emergence of fruits, were all carefully illustrated and described. In fact, the descriptions of trunk variation and peculiarities to be found in Chapter II and elsewhere need but little amplification here, and need not be repeated. Placed in simple order, according to their value in determining species, the *tout ensemble* of characters of a fossil cycad is as follows:

A. Fruits: (1) stamens, (2) seeds, (3) receptacle, (4) bracts, (5) ramentum.
B. Woody cylinder and medulla: (*a*) dimensions in longitudinal and transverse sections, with structure details; (*b*) growth rings when present.
C. Cortex: leaf-base traces, peduncle traces.
D. Armor: leaf-bases, ramentum, fruit-series.
E. Leaves: Rachis, pinnules (with form and insertion).

This arrangement is more than a mere enumeration. It expresses quite accurately the relative value of the Cycadeoidean structures, floral and vegetative, in species determinations, bearing in mind of course that fruits, especially the staminate disks, are seldom present; though fortunately the young crowns of leaves are more abundant than at first supposed. In Volume I (p. 8) it is recorded that the majority of the trunks of a lesser

collection now belonging to the American Museum of Natural History bear crowns of young leaves. Large sections would not infrequently reveal crowns not exteriorly visible and laterally borne fronds have been observed in four different species.

When staminate disks, the structure of which can be made out, are present, the parts afford as convenient and reliable specific indices as do the floral structures of angiosperms. Thus in the case of a steadily increasing number of trunks there is being accurately determined not only the general appearance and size of the stamens, but the number entering into the disk. Furthermore, the meaning of such flowers is becoming clearer as more and more of the related Williamsonian flowers are brought to light, affording comparisons of the very deepest interest. Not only so, but taking the *Cycadeoidea* flowers as a whole, they have the essential complexity of the flowers of the simpler dicotyls like the magnolias and are sure to be found in great variety as time goes on, the strong probability being that the disk or campanulate type is distinctly specialized and ancient. Whether or not new disk types are actually found among the cycads with large trunks, relatives will at least be found in large numbers, showing very distinctly variant types of free stamens and many modifications of the central strobilus.

It is, however, the woody cylinder of the trunks, when all the dimensions are considered conjointly with full measurements of the complete longitudinal and transverse sections, which must yield the surest specific indices in most instances, more especially in those of most interest in comparisons with other gymnospermous woods. It is not, however, to be inferred that it is always possible to determine species on the basis of wood structure alone. In the first place, no such searching and ultimate study has as yet been given to any trunk as to now make this possible; and, secondly, there are too many instances where structure is more or less lacking in clearness; while even in the case of trunks of existing conifers determination of species from microscopic sections is plainly difficult to carry out. Such attempts have indeed been made, but it is by no means a matter of record that the accuracy of the schemes or diagnoses proposed has been verified in practice or soon will be, without laborious revision and extension.

The thick cortex is a further very characteristic feature of the Cycadeoideans, and the oblique section traversing the cortex so as to cut the leaf and peduncle bundle traces affords one of the very best specific indices. The size of the cortical traces agrees with that of the mature fronds and thus comes to vary markedly in the different species, so that the cortical sections at once show both the bundle pattern and bundle strength in many cases where the outer appearance of the leaf bases leaves one wholly in doubt.

Finally, the armor is that particular region of the trunk which has furnished most of the characters on which species have been from time to time established; that is, the outer region, where the characters are the least distinct, owing to the different types of conservation and the varying extent of erosion and compression, has necessarily been the region first appealed to in founding new species! But that these species, based mainly on the superficial characters, can have only a general value in the limited number of instances where there are very broad differences in the size of the leaves and the quantities of ramentum present, has been fully explained in Volume I, where it has been made clear that in the great majority of trunks the tangential sections of definite diagnostic value must be serial, must include three or four lesser parallel sections a centimeter or so apart, or be of such large size as to yield what are virtually series of sections of the leaf bases from the insertion on the cortex out to the ends; also, such sections must be cut from the basal, mid, and apical regions of the trunk.

Naturally, in using the more obvious criteria of species, or set of characters found in a given species, many points of doubt will arise, many instances must occur where the evidence is so nicely balanced that a decision is liable to be based somewhat on general impressions rather than actual differences; nevertheless, in practice it should be possible to split the various groups of cycad trunks into approximately true species, and to this task we may now turn. Firstly, the simple-stem group of the Piedmont-Black Hawk region is taken up, then the simple-stem groups of Maryland and Wyoming, so far as this is feasible; secondly, the great branching series of trunks from Minnekahta is considered at length, and then, following the record of isolated trunks, several descriptions and comparisons of important European forms are profitably given. Finally, after a more adequate study of Cycadeoid seeds, a subject noted as of special importance in the preface to Volume I, the Williamsonian series is taken up at considerable length. Just as the silicified cycads were compared with the existing forms in Chapter IX, Volume I, so now it will be found practicable to go on and institute interesting comparisons between the Cycadeans, Cycadeoideans, and Williamsonians. The latter were previously far too little known to permit any extended treatment, but are now so much better studied and afford so many missing links, going far toward clinching the proposition before maintained that the Cycadeoideas and their relatives are true cycads, that the results brought together should justly be the chief feature of this volume. Thus will be made possible a closer summary of progress achieved in the re-presentation of the Mesozoic cycads.

As will be observed, therefore, the present work is neither in subject-matter nor plan in any sense a repetition, but strictly a continuation of the structure volume, with this difference: Whereas in that work the results of previous cataloguing and assignments of species were at all points accepted without question in order to avoid a later confusion, the effort will now be made to question specific values and priority; at all points it will be sought especially to lay the foundation for a better and better taxonomy. For this very reason, the use made of the data brought forward can not be final. In a certain sense the earlier work was complete in itself because its scope was confined mainly to the description of elements of structure, that could at least be illustrated with a fair degree of fullness by drawing on many trunks for evidence. Categories of new structural facts are fairly fixed. But now the descriptions are to be closely restricted to individual trunks or to those considered specifically equivalent, and all the old features as well as those here described for the first time are to be used as far as feasible in specific determinations which it is very certain must long be liable to revision and change, not only as more and more searching studies of the immense store of material already at hand are made, but with the fortuitous accumulation of new and perhaps much better collected material, especially if obtained in groups, to say nothing of changing views of the criteria of cycad species.

While, then, the presentation of structural facts hitherto unrecognized has much of permanence, classifications are after all partly modes of attack and partly ideals toward which we strive always, being in their earlier, less-elaborated forms strictly temporary, particularly so in the case of highly organized forms like those before us. Even though one had prescience he could not make classification final in a fossil group where so much of the evidence is either inaccessible or hidden; but the incompleteness and the tentativeness of classifications do not necessarily detract from their value. Taxonomies are set forth for immediate use, and can not therefore be fairly tested by the length of time they endure. Their excellence thus rests mainly in their clearness rather than their particular form, their value being greatest if in the course of use they lead to the minimum amount of confusion and change.

Because of such considerations, it will be the aim to pursue a mean course. As far as possible, descriptions of species will be rested on structures found in notable specimens, and large numbers of specimens either wholly unstudied or lacking the more usable criteria will necessarily be passed by. Only in this manner can the specific determinations already brought forth be least disturbed; and this we hold to be the clearest method of procedure. In short, in drawing attention to histologic features, and more or less plainly showing the insufficiency of any macroscopic methods of cycad determination previously applied, it will be the constant aim to avoid setting up other equally imperfect standards of species. The position in which a student of cycad structure at present finds himself is by no means so clear and simple as would be, for instance, the position of vertebrate paleontologists, were it to become possible for them, through some fortuitous discovery, to study the myology and reproduction of groups of Permian vertebrates or of Jurassic and Cretaceous mammals. For skeletal indices, even though incomplete, are quite fixed in character and their description is a permanent contribution; while here the species and genera now fairly incorporated into the literature are largely based on external characters too variable for other than a most limited use. It is no exaggeration to say that most Cycadeoid species have been based on the characters which are the most liable to individual variation in life, the least diagnostic of species, and the least susceptible to constancy of preservation. Yet I doubt if it would be even a temporary advantage if we had the means of arbitrarily casting these determinations aside and beginning anew. They include, in the clearest manner, the history of cycad study and are therefore undetachable parts of the record.

My own view of the value of these species, European as well as American, gained from long study of thin sections, thus remains unchanged. More than ever it appears, as expressed several years ago, that the arbitrary use of macroscopic characters has been in the main justified. This is merely the time-honored method of following the line of least resistance. The collection catalogue, however artificial, is after all indispensable to later and more exact study. It may be held fortunate that few persons have shared in naming the American Cycadeoids; for our specific series probably has more of homogeneity than has the European series, which, though based on far less material, is quite as long and is established on characters even more arbitrary and difficult of application. It is also fortunate that so far there has been in America an avoidance of that plethora of generic names which, though serving as an adumbration of what the future must surely bring forth, is as yet unfounded on definitely determinable or applicable structural variations. Unquestionably a fairly felicitous treatment of these overlapping genera requires both patience and acumen on the part of the investigator with new or relatively unstudied material in hand.

The main point necessary to bear in mind in the present connection would seem to be that, in the case of the cycads, specific determinations bearing the stamp of finality can only be approached more slowly than might at first be assumed from the wealth of critical structures. It is but natural that the first question should be, just as one might ask in the case of an ammonite, what is the species; but it is no evidence of lack of progress in these studies to point out that the demand for specific identification should not be too insistent, since the actual specific position of large numbers of the cycad trunks must long remain in doubt.

The species which may be included in the genus *Cycadeoidea*, or eventually divided into several closely kindred genera, represent a really rich assemblage of forms. So far as the various trunk series have been examined, whether columnar or branching, they have always suggested the presence of much specific variety, usually confirmed by later study. It is therefore easy to see just why determination of such small units as true species must

long prove a more or less baffling task, an ideal which may be approached and at last nearly but never wholly realized. If one had placed before him an assemblage of a dozen to a score of oaks, or better, of present-day cycads more or less fragmentary and stripped of foliage and fruits, specific assignment would be difficult enough. But because first one feature or group of features and then another is conserved or visible, it results that one is continually faced, not only by multiplicity of features, but by varying series of structural details. When, too, the variations of fossil preservation in different localities and periods add other difficulties, specific determinations merely become a goal toward which to strive. It is therefore of the greatest importance to present structural details as rapidly as these can be assembled, with as little of specific rearrangement as possible.

It may be frankly confessed that several years ago the writer held much larger expectations of early and rigid definition and measurement of species, but it is now seen that it is not feasible to move so rapidly, and that it is first necessary to present in the simplest manner the facts and details which have been accumulated as nearly as they can be related to the several species. Gradually, serial sections from wedges of the best-conserved trunks will be accumulated, and no doubt the results at first easily deemed near to consummation will be accomplished as one of the final and ultimate results of the study of silicified cycads.

CHAPTER III.

SYSTEMATIC POSITION OF THE CYCADEOIDEÆ.

The position of the Cycadeoideæ in the natural scheme or classification, the one which so far as feasible includes living and fossil forms of any kind arranged in their approximately true juxtaposition and thus indicates probable lines of descent, may be simply shown. This fact was not quite so clear when Volume I was published.

As will appear in the later chapters, the Williamsonians are even more closely related to the Cycadeoideæ, and both these groups to the Cycadaceæ, than was at first understood. The very notable anatomical studies of Matte show the presence of hypocotyledonary centripetal wood and other primitive features in the Cycadaceæ and lead to the conclusion that the existing cycad trunks are unquestionably derived from Medullosan forms, also recalling *Lyginodendron*. In addition to the studies of Mexican Williamsonias, Chamberlain has shown the presence of growth rings in *Dion*, just as noted in *Cycadeoidea*, as well as the numerous staminate cones in the leaf axils of *Bowenia*, and the laterally borne, bract-inclosed peduncles of *Macrozamia Moorei*, agreeing outright with *Cycadeoidea*. As Coulter and Chamberlain state the case, even before the accumulation of Chamberlain's later notes and more crucial observations, "the Bennettitales and Cycadales have a common origin and are more intimately related to one another than to any other gymnosperm group," it being evident that "reasons for keeping the two groups separate are more necessary than reasons for claiming that they are genetically related." This sustains the earlier contention.

Taking, then, recent and telling discoveries emphasizing community of origin and similarity of structure in the existing and fossil cycads, there does not appear to be any need to depart from the conclusion reached in handling the evidence brought together in the first volume, that all the forms are best included in a single great group, the Cycadales. This group is then normally attached to Coulter and Chamberlain's Cycadofilicales as its full evolutionary antecedent—a group which occupied a great stretch of geologic time and was doubtless fully as varied as the Cycadales taken in the inclusive sense here preferred.

It has been obvious, from various texts which have appeared since the publication of Volume I and later studies, that many botanists have been somewhat loth to admit the fossil cycads into a position in the Cycadales, partly on structural grounds and partly from the view of supposed convenience. But if some able botanists view the Cycadales as inclusive of the great fossil assemblage of cycad-like plants, these latter can not be separated from existing cycads by any very great structural hiatus. Not only so, but this flexible use and extension of the group term Cycadales has been made further logical and convenient by Professor Nathorst's introduction of the still more elastic term Cycadophyta, used for all plants with cycad-like foliage. In addition to this handy term, the simple and self-explanatory expression *Cycadeoids* is here proposed for the sub-group of plants included in the family Cycadeoideæ and all those other fossil forms which have a more distinct affinity to this family than to the existing cycads. When speaking of cycads without other qualification we primarily mean existing cycads, but may include in this simple term all cycads, that is to say, all Cycadophyta. The Cycadophyta therefore include: (1) the existing cycads and such fossils as with them make up the Cycadaceæ; (2) the Cycadeoids or Cycadeoideans

plus all the members of the Williamsonian tribe; (3) the various genera of very doubtful position and affinity, like *Dioönites*. The latter, as Professor Nathorst was able to show, must have had a very singular and primitive staminate inflorescence characterized by peculiar "antherangia," which even suggest the presence of a great group, the "Dioönitales." But it is very well understood by all botanists that even a considerable number of the forms conveniently called Cycadophytans must be generalized types. Thus Professor Nathorst has also shown that the loosely compacted strobilus with very leafy two-seeded megasporophylls called *Cycadocarpidium* (196) pertains to leaves of *Podozamites* aspect, but borne spirally on small scale-covered stems of presumably limited growth and distinctly coniferous habit, this being perhaps the first form ever determined from that unknown borderland between cycads and conifers.

When we come to the division of all those better-defined and more clearly understood members of the Cycadophyta, existent and extinct, the needs and the usages of classification are still plain. Carruthers's division (1870) of the fossil and existing cycads into four equivalent families, the Cycadeæ, Zamiæ, Williamsoniæ, and Bennettiteæ, is still adequate, except that the last of these four names is not admissible or tenable from any view whatsoever. It is antedated just 42 years by Robert Brown's Cycadeoideæ, used in precisely the same sense and a family name which could scarcely be more expressive or happily chosen, a name which sprang from a certain prescience which at times goes far to make taxonomy a living, moving force and weapon of the investigator. This is in no sense a criticism of Carruthers; quite the contrary, he accepted the evidence gained from a wide study of the cycads existing and extinct, and effectively stated the facts as he saw them, but he did not have before him the superb Italian series of Cycadeoideas or the great American collections equaling and surpassing in number and perfection of conservation all the cycads of the world beside.

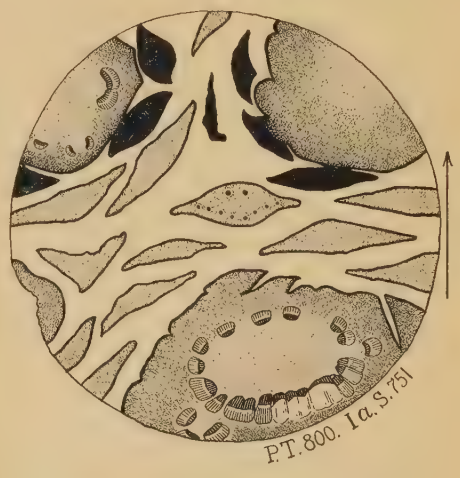


FIG. 2.—*Cycadeoidea* (*Bennettites*) *portlandica* (?). Yale section No. 751, cut from a cylindrical core. Natural size.

No other than specific differences from American trunks can be pointed out in any of the various sections thus far cut from the Isle of Portland trunks. This section traverses the basal region of the armor, cutting three lesser branches or peduncles of large size, the basal bracts (?) of which have the size of lesser leaf bases or scale leaves. In fact, a gradation into scale leaves is indicated, and these may even have borne pinnules such as are found in the lesser vegetative bud or branch crowns of *Cycadeoidea Dartoni*. (*Cf.* Fig. 3.)

Perhaps the fact which has tended most to obscure the necessity for avoiding confusion by the use of Brown's Cycadeoideæ has been a certain difficulty in laying hands on precisely the original types of *Cycadeoidea* figured by Buckland. These unfortunately are not found among the definitely labeled collections of the British Museum or other English museums.*

*From the new British Museum Catalogue of the Cretaceous Flora, Part II (Stopes, 320*b*), which only reached my hands after the present manuscript was completed, it is learned that the whereabouts of the Buckland specimens still remains unknown. It can hardly be doubted that these specimens are in some private collection which has not been subjected to study during the past fifty or sixty years. Unfortunately, no mention dependent on direct examination of the specimens appears in any contributions made since the time of Buckland. The interest of these types is so great that the Buckland figures and descriptions should be supplemented in the light of later study and republished. It is probable that this would lead to a successful search amongst some of the older English collections and that interesting duplicates may also be found.

In this new catalogue Dr. Stopes tenaciously insists on the use of the Bennettiteæ as the inclusive family name for Cycadeoidean trunks with fructifications. Further mention of the arguments advanced is given on a later page

But it is very improbable that they have been lost, and doubtless a more prolonged search or some fortunate accident will presently reveal these finely conserved and excellently figured historic types. Meanwhile it is possible that some of the sections prepared by Witham and figured by Buckland in the Bridgewater Treatises, being the first ever cut from petrified cycads, are included in the British Museum collections at South Kensington. These sections are adequately figured on Plates 61 and 62 of the Bridgewater Treatises, which clearly illustrate the typical *Cycadeoidea* structures with but a few of those minor discrepancies to be expected in the drawings of histologic structure dating 80 years back. Even so, the drawings nicely indicate the strengthening of the leaf-base bundles on the superior side, so characteristic of *Cycadeoidea*, while the cortical bundles of pronounced horseshoe type, with rarely a completely inclosed or true concentric bundle, are unmistakable. The transition or splitting up of these bundles into the lesser bundles of the leaf-base series is likewise evident; also the somewhat flattened peduncle bundles, giving rise to the lesser horseshoe bundles forming the bract supply. In fact, these sections could just as well have been prepared from one of our western Cycadellas, if not indeed from *Cycadeoidea Dartoni*.

FIG. 3.—*Cycadeoidea minnekahtensis*. (Ward det.) ×⅛.

This fine specimen was originally No. 242 of the Yale collection from Minnekahta, South Dakota. Later transferred to the botanical department of the University of Cambridge, England. The specimen weighs 104 kg., and clearly illustrates the transition from columnar to branching forms. A medium-sized lateral branch *B*, with clearly outlined medulla, is broken away, as is also the summit, which evidently consisted of several branches. A few ovulate cones 3 cm. in diameter are present, but some of the smaller axes, as at *b*, are probably vegetative buds exactly comparable to those of the *Cycas* illustrated in figure 5 and so numerously borne in the much-branched plant of figure 7. (See description of *Cycadeoidea Dartoni*.)

Not fully realizing the excellence and value of his earlier description, Buckland calls the specimens of *Cycadeoidea* figured in the Bridgewater Treatises *Cycadites*, a change not merely unnecessary but inadmissible. As Seward has shown, the *Cycadites* of Sternberg (1825) can only be applied to fronds of uni-nerved type, like those of the genus *Cycas*. Also Unger, in the *Genera et species*

under the caption *Bennettites Gibsonianus*. From the remarks there recorded the reader will learn why it is not deemed necessary to change in the slightest degree the conclusions already reached. Neither will the introduction of the new genus "Colymbetes" tend to simplify matters. The proposing of new genera which can not be sharply differentiated from imperfectly studied genera already established in scientific literature is sometimes difficult to avoid; but it is probable that *Colymbetes* is a synonym. The covert suggestion that there might be reasons for discarding *Cycadeoidea* altogether can hardly be expected to appeal to extra-English paleobotanists.

plantarum fossilium (1850), so defines *Cycadites;* and not even the fronds of *Cycadeoidea* can be placed within this frond genus. However, it is clearly and precisely the original species *Cycadeoidea megalophylla* and *C. microphylla* which Buckland refigures. This fact has not always been admitted, although it is perfectly clear that Buckland knew his two entirely valid species well. A slight error in the scale of size for the later drawings, which are marked as one-half of the natural size, quite clearly shows them to have been

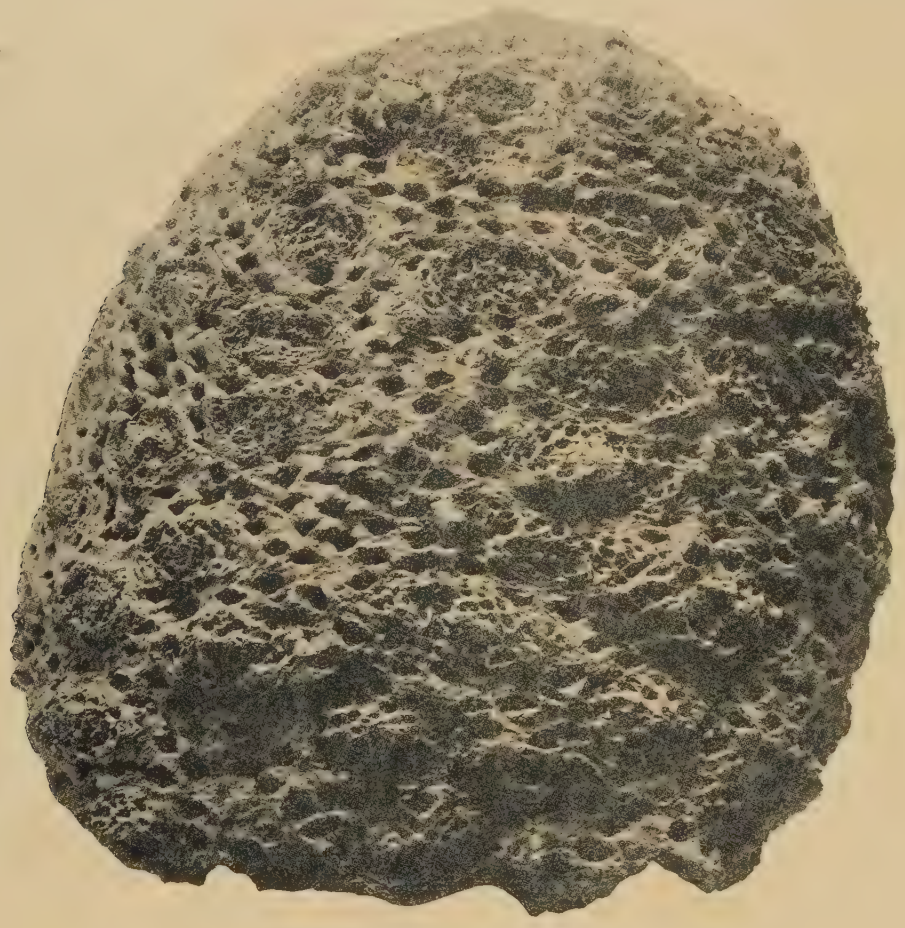


FIG. 4.—*Cycadeoidea dacotensis.* Weight 70 kg. ×0.2.

This Minnekahta (South Dakota) specimen was originally No. 212 of the Yale collection, but is now in the Natural History Museum, Stockholm. An interesting feature is the fine crown of young fronds accompanied by the well-advanced and numerous fruit series, affording a certain contrast by its growth stage as compared with that of a stem like *Cycadeoidea Dartoni* with an immense number of mature cones and not the slightest indication of further leaf growth, the terminal bud being wholly made up of scale leaves. It is desirable that the record of flower-bud and leaf growth should be kept in order to determine, in the course of time, whether pollen and seed maturation were confined to a single season or not. The first recorded instance of flower buds accompanied by an approximately half-grown crown of fronds is the great type of *C. ingens*, where, however, testimony is inconclusive, because relatively few floral axes are present, and it is less certain that a final fruiting season is indicated.

made from the two original forms. For it is at once seen that the drawing of the transverse sections through the *C. microphylla* leaf bases are about correctly marked as to size, while the trunk figures are merely given half the size shown in Buckland's paper of 1828 on the Cycadeoideæ, a family of fossil plants found in the oölite quarries of the Isle of Portland. In this paper the trunks are shown *reduced one-third*, so that the later figures, which are both marked one-half the natural size, are really only a third natural size.

A striking feature of these later illustrations is the careful indication of the numerous lateral fructifications, entirely omitted from the far more generalized preliminary drawings and betraying painstaking effort to show the actual features of the specimens. (Compare the accompanying text-figures 2 to 7, noting the supplementary details they finely afford, showing the nature and extent of budding, branching, and fruiting in the cycads and cycadeoids.)

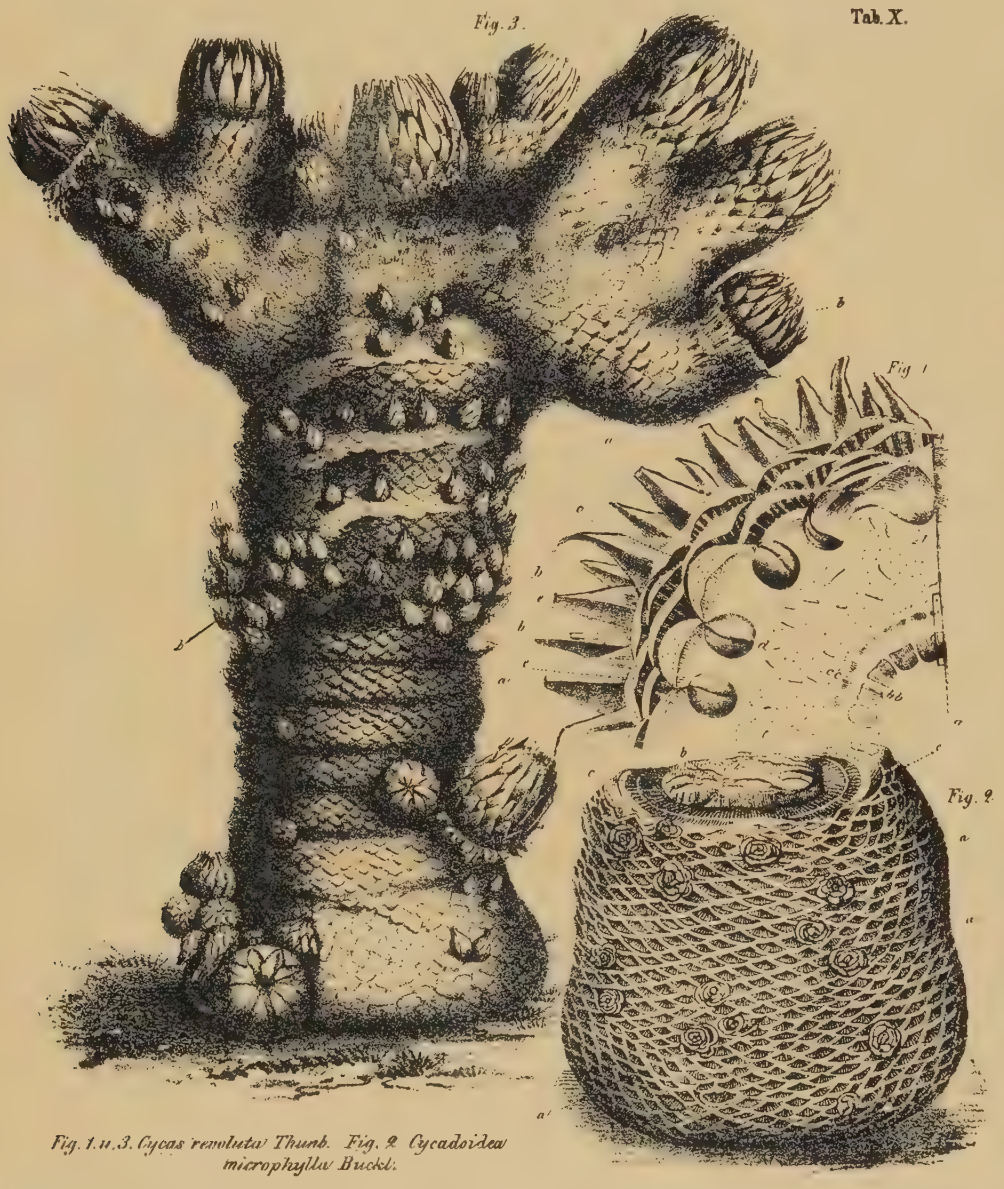


FIG. 5.—An old Javanese *Cycas revoluta* (fig. 3) bearing numerous scale-leaf enveloped branches and small scaly buds, as validly compared with *Cycadeoidea* (Fig. 2) by Göppert 62 years ago.

Plate X of Göppert's Denkschrift of 1853 is here reproduced in entirety because of the most felicitous manner in which it illustrates the close similarity in the branching and fruiting habitus of existing and fossil cycads. A freer basal production of fruits in the latter is in reality the only difference. The full extent of the comparison is made clearer on reference to figures 4 and 7. Figure 1 is a transverse *Cycas* stem section. The plate-figure 3 is originally from Vrolik (1846), and 2, showing *Cycadeoidea microphylla* from the Isle of Portland "dirt bed," is from Buckland.

Buckland also expressly mentions that Robert Brown had seen one of the "silicified buds"—unquestionably a flower bud—and it is certain that the specimens exhibiting such features were much above the average of conservation for Isle of Portland specimens. As will be recalled, the Portland quarries had yielded these "crows nests" of the quarrymen from the days when the stone for St. Paul's was quarried from beneath the cycad-yielding "dirt bed."

Later on Brown observes in the English trunks the very features now known to indicate both diffuse and close-set fructification, with true monocarpy, as better exemplified by American specimens. He says, as quoted by Carruthers in establishing the new genus *Bennettites*—"all the specimens of *Cycadites* hitherto found in the Isle of Wight agree in having an elliptical outline, unaccompanied with any inequality in the woody ellipsis, and also in having a bud in the axilla of each leaf; in these respects differing from the *Cycadites* of the Isle of Portland and from all the recent species of *Cycadeæ* with which we are acquainted, which have a circular outline and only scattered buds." (Brown 39, Carruthers 51, p. 695.)

This observation is very interesting; but the longer the Isle of Portland trunks are studied, the more abundantly are they found to bear fructifications or at least peduncles of the usual Cycadeoidean type. Besides, many of these trunks are found in the upright position in the "dirt bed," with their summits crushed down, a fact which in itself greatly limits fruit conservation, since the basal region of Cycadeoidean trunks bears far fewer fruits than the upper and apical region. Consequently, the Portland series of trunks always gives one the impression of bearing fewer fruits than must actually have been present. Contrariwise, in the Black Hills series the upper half of the trunk is so frequently the better conserved as to give one the immediate impression of an exceedingly fertile series. The *Bennettites portlandicus*—which is, of course, very near to the *Cycadeoidea microphylla* Buckland—is a fine example of a "dirt-bed" trunk conserved more in the manner of American specimens with a very striking series of fructifications or peduncles. (*Cf.* Carruthers, 51, pl. 61.) Yet such specimens have not deceived Carruthers himself, and he is by no means inconsistent in his interpretation of an English specimen figured by Corda when he goes on to say:

> "Corda, in his 'Beiträge zur Flora der Vorwelt' (tab. 17, p. 38), figures and describes the fragment of a fossil cycad which he supposes came from England, and to which he gives the name of *Zamites Bucklandi*. It consists of a small portion of a stem from the woody axis to the surface, like rolled and broken fragments of both the Isle of Wight species which have been found on the shore at Brook. There are no indications, in the complete and evidently accurate drawings, of any secondary axes; but the form of the petiole, the arrangement of the vascular bundles, and the abundant ramentum between the petioles (which Corda considers to be intermediate or sterile scales), as well as the general form of the fragment, clearly show that it belongs to the genus *Bennettites*. Were it not that the petioles are in section so distinctly quadrangular and so small, I should not hesitate to refer it to this species (*B. Saxbyanus*)." (51, p. 699.)

This explains clearly enough why American and European paleobotanists have invariably found it necessary to refer their material back to the Buckland genus *Cycadeoidea* and Brown's family the Cycadeoideæ. Much more, throughout the study of American fossil cycads, close attention to European material has been continually given and the series of Isle of Portland specimens—from which trunk sections, cylindrical cores, and thin sections have been cut—doubtless falls but little short of that in the hands of anyone; nor has any sufficient reason yet been found to indicate that the two trunks figured by Buckland are not thoroughly characteristic for the great majority of Isle of Portland specimens. That one of these specimens may have differed generically from the other is another point

altogether. Buckland's description suggests a polyxylic wood zone for the *C. microphylla*, but must be somewhat in error. No mention is made of the base, and the appearance of wood rings at the summit as figured is much better explained as merely a well-separated xylem and phloem. That Robert Brown found scalariform wood is stated in a later note.

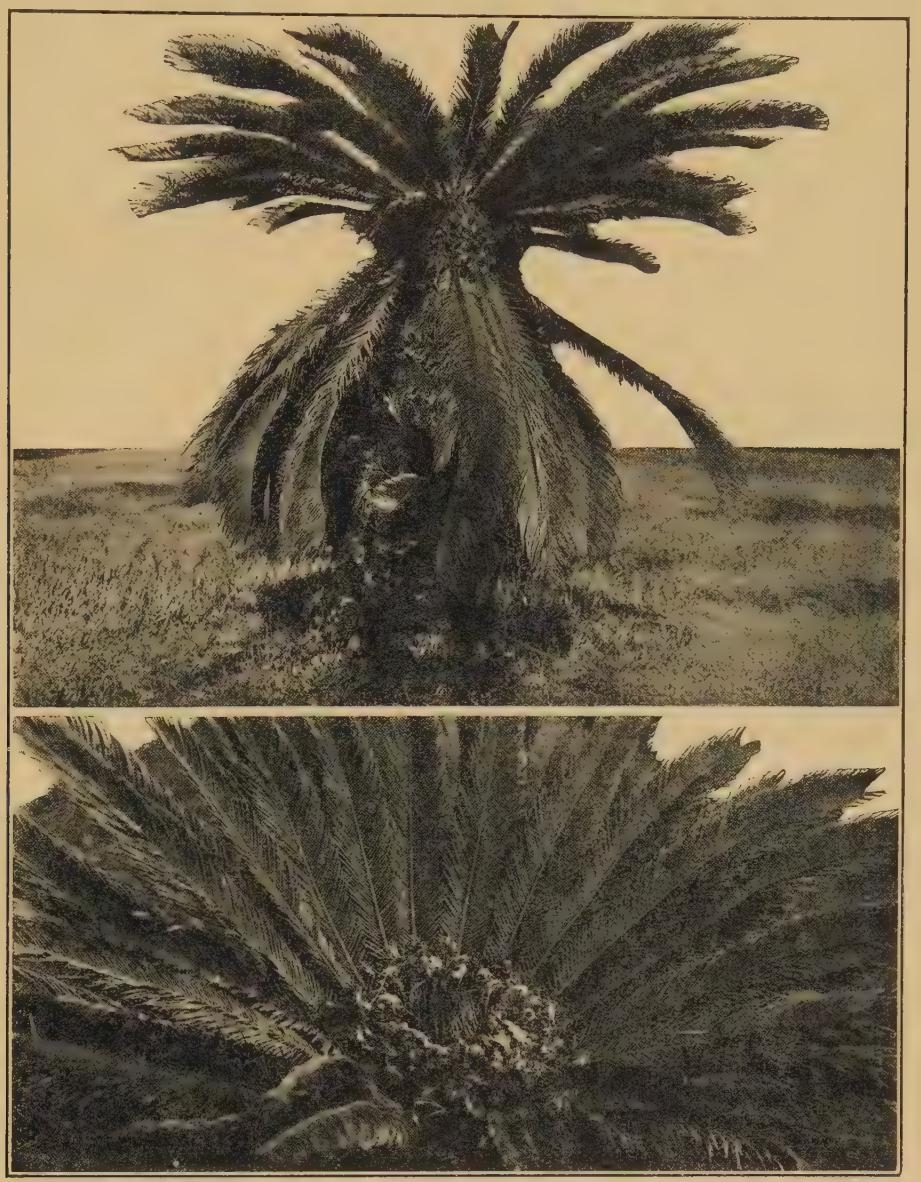


FIG. 6.—*Cycas revoluta*. Ovulate plants, Florida.

The scale leaves precede and protect the foliage and carpellary leaves, the stem being as truly nodal as that of the Williamsonias or the lesser branches of magnolias or pines. In the lower plant the apical cone of scale leaves still incloses the new crown of foliage leaves; while in the upper plant a succeeding crown of foliage leaves has reached full size with the old carpellary series and the scale leaves between the two full-sized leaf series. A lesser feature of the upper plant is the occurrence, near the base, of vegetative scale-leaf covered buds, sometimes producing smaller fronds just as in *Cycadeoidea*. There is in the Cycads and Cycadeoids every stage between the tree-fern-like condition, with all foliage fronds and the regular alternation of scale and foliage leaves. In most robust forms the nodal character is suppressed, but in the slender-stemmed Williamsonias it becomes quite as pronounced as in conifers and dicotyls. In the conifers groups of both ovulate and staminate cones appear in relatively the same position as the carpels of *Cycas*, the axis continuing to grow.

Owing then, it appears, to the fact that the great majority of the Portland specimens are vertically crushed and of such rough exterior, an adequate study of the series has never been carried out and the excellent conservation of not a few of the trunks seems not to be generally known. Nevertheless, it is clear from the later drawings that Buckland had selected for his types two of the more finely conserved forms—those rarer finds like the much later *Cycadeoidea gigantea* of Seward (274), which only long periods of perhaps 50 or even 100 years bring to light at the Portland quarries, trunks in every respect as perfect as and agreeing with the Black Hills Cycadeoideas. It is also very interesting to compare these drawings with the Göppert figures of *Cycadeoidea* (*Raumeria*) *Reichenbachiana*, the wonderful Dresden specimen, published 16 years later, but scarcely as satisfactory.

It results, in fine, that the validity of *Bennettites* as a generic name is entirely outside the larger question of taxonomy here discussed. *Bennettites* may or may not be distinct from the genus *Cycadeoidea*. In my judgment, after long study of both the European and American specimens bearing on this question, the chances are that the fruit of *Bennettites* does not differ generically from that of any of the *Cycadeoidea* fruits thus far discovered; nor does the remarkably well-conserved wood structure of the Isle of Wight specimen afford any surer means of generic separation from the Isle of Portland trunks.

Whether it will be eventually desirable to separate the already large genus *Cycadeoidea* into various well-defined genera is also beside the point at issue; any such separation must rest on characters exhibited by trunks as yet little studied. The trunks most likely, in the course of time, to require removal from the genus *Cycadeoidea* are primarily the American specimens from Black Hawk, which exhibit heavy wood zones with far more distinct growth lines than those of the existing *Dion*. It may, however, be reiterated that in 1907, after considerable study of European specimens, with the determination for the first time of the entire agreement of the fructification of *Cycadeoidea etrusca* and *C. Reichenbachiana* with that of the American Cycadeoideas, the conclusion was reached that the only possible way to avoid much confusion in the nomenclature of fossil cycads was to discard the family name Bennettiteæ altogether and relegate *Bennettites* to the position of a doubtful monotypic genus, just as Capellini and Solms, and after them Ward, as well as several other paleobotanists, had already definitively done (386). The simple fact is that, while the original types are English, all the material of critical value studied in recent years is extra-English, and there seems no reason to depart from the following conclusion:

"*Cycadeoidea Reichenbachiana* adds another member to the long series of trunks extending from columnar types (which have mostly, though not always, large leaf bases) to the great branching types from America, characterized usually by leaf bases of moderate or small size. Moreover, while *C. Reichenbachiana* is a columnar form, its flower bud agrees closely with that of the branching cycads of the Black Hills, especially *C. dacotensis*. In the light of these new facts concerning long-known European cycads, the family name Cycadeoideæ used by Robert Brown (1828) certainly includes all the forms which English writers on fossil plants have much later mistakenly placed in their so-called Bennettiteæ. Similarly, the proposal that *Cycadeoidea* (1827) shall be the generic term used for stems without recognizable fructifications can not be accepted, for the simple reason that not only are the Buckland specimens vegetatively like the other trunks from Europe as well as the American forms, but, to go no further than the evidence afforded by the original descriptions, the tangential section figured by Buckland eighty years ago clearly shows a large and characteristic peduncular bundle. As to the genus *Bennettites* (1867), this can at the very most include two or three species, so far as known, the great majority of the species of Cycadeoideæ falling within other genera. And so far as truly problematic trunks of unknown fructification and really doubtful vegetative characters are concerned, it only needs to be remarked that there is already at hand, for their reception, a plethora of such names as *Yatesia, Withamia, Becklesia, Fittonia, Clathraria, Cylindropo-*

dium, and *Bolbopodium*. It would certainly be as illogical to insist that we relegate to a minor position a correctly used generic name for the sake of a handy nomenclature for cycad trunks without distinct or distinctly conserved fructifications, as it would be to say that we can never learn the fructification of a fossil the vegetative features of which are the first to be discovered, or are, as in this case, the *first to be understood*. Clearly, therefore, those who would further use the family name Bennettiteæ, or the generic name *Bennettites*, in other than a wholly restricted sense, must err in both these respects." (386.)

Ordinarily a mere question of nomenclature would scarcely merit such a detailed consideration as that just given; but owing to the striking character and cosmopolitan distribution of the Cycadeoideæ, and the great amount of study which has already been devoted to and will long continue to be devoted to this family and its relatives, the first desideratum is to reach some reasonable degree of nomenclatory precision. With the family and generic names now fairly established, it only remains to mention briefly the ordinal position of the Cycadeoideæ, purposely left till last in this discussion.

FIG. 7.—*Cycas revoluta* ♂. Photograph by Stopes.

A single much-branched staminate plant, about 5 m. in height, with a habitus simulating the "Knieholz" (*P. pumilio*) or the American Mughus pine. Yejiri, Japan. Some of the many large curving branches are supported by strong props. In addition to huge staminate cones, all the larger branches bear innumerable small scaly buds, at first seated directly on the old leaf-bases in the axillary position, but having the power to produce leaves and develop a woody cylinder connection. These buds also readily produce roots. Compare figures 8–13, 104, of Volume I.

Potonié was the first to propose the segregation of the Bennettitaceæ as typifying the greater group Bennettitales; but, like any adventure into the taxonomy of fossil gymnosperms not based on the direct and continued study of new material, the Potonié classification has a rather doubtful value. As already emphasized, there appears to be no necessity, either structural or of convenience, for regarding the fossil cycads which go to make up the Williamsonian or any of the silicified series as non-cycadalean. An ordinal rank for this varied and remarkable but homogeneous assemblage of Mesozoic plants has not been in reasonable doubt at any time since Carruthers first discovered the striking type of the ovulate fructification in his *Bennettites Gibsonianus* 45 years ago. Whether happily chosen

or not, the order Bennettitaceæ of Potonié has priority for the present and in any case expresses a natural division of Cycadeous plants, as appears in the subjoined classification.

In giving this new classification, it is realized keenly that a rigidly exact set of boundaries is impossible at present, and probably never can be given in the case of many of the genera and some of the families and orders; but even a casual examination of the order in which the genera are aligned will show a gradual passage from the more specialized and better-known types to more and more generalized and finally problematic forms. The arrangement is intended to be elastic and may prove more usable than previous classifications, in helping us to gain a better general conception of the structural features of the great cycad phylum and its immensely varied distribution in latitude and time.

Cycadophyta	Cycadales	Cycadaceæ (Cycads)	Zamiæ	(*A*) Zamia, Microcycas, Ceratozamia, Dion.
				(*B*) Encephalartos, Stangeria, Macrozamia, Bowenia.
			Cycadeæ	Cycas.
		Bennettitaceæ (Cycadeoids)	Cycadeoideæ	Cycadeoidea.
				Bennettites, etc. etc.
			Williamsoniæ (the Williamsonian tribe)	Williamsonia.
				Wielandiella.
				Anomozamites.
				Ptilophyllum.
				Otozamites.
				Pterophyllum.
				Glossozamites.
				Dictyozamites.
				Plagiozamites.
		(incertæ sedis)	Podozamiteæ	Podozamites.
				Plagiozamites.
				Sphenozamites
			Pseudocycadeæ	Pseudocycas.
				Cycadites.
				Stangerites.
	Nilssoniales			Ctenis.
				Ptilozamites.
				Nilssonia.
	Dioönitales	Dioönitaceæ	Dioöniteæ	Dioönites.

CHAPTER IV.

THE MARYLAND GROUP OF CYCADEOIDEAS.

Just as the Isle of Portland Cycadeoideas, brought to notice by Buckland in 1828, represent the oldest of the European silicified trunk series, so the cycads of the iron-ore beds of Maryland, as first noted by Tyson in 1860, form the oldest American group; and there are many and notable points of resemblance between these two striking and homogeneous assemblages of silicified Cycadeoideas. The Portland trunks vary all the way from the crushed and nearly shapeless "crow's nests" of the quarrymen to superb columnar specimens like *Cycadeoidea gigantea*, and are found in approximately the same positions in the Portland "dirt bed" in which they must have grown; while the Maryland cycads, though occurring more sparingly in estuarine situations, show a far more even type of conservation, most of the trunks being uncrushed and retaining their macroscopic characters in clear detail. Here, however, the noteworthy differences cease. In both groups there are relatively few species and the trunks are for the greater part young and without distinct or conserved fruits, although in both cases such occur occasionally in considerable abundance. Moreover, the species of the two series are so closely related that, whatever may be said of the validity of the six or more Portland species and the nine species ascribed to the "Iron Ore Beds," all the forms belong with certainty in the same section of the family Cycadeoideæ in so far as any of the features, histologic or macroscopic, thus far observed enable us to judge.

In both cases, too, the trunks have suffered considerable maceration, which renders the thin sections, at least at first sight, rather disappointing and difficult of study; and certainly the remarkable conservation exhibited by *Cycadeoidea Reichenbachiana*, the Italian trunks, and even the more or less crushed trunks of the "Freeze Out Hills," is not likely to be found in any Portland or Maryland cycad. But too much must not be made of the lack of preservation in these forms. More recently a searching study of what at first appeared to be a much-macerated portion of a Cordaitean log from the Indiana "black shale" revealed the presence of a small interior area, of but a few cubic centimeters, so remarkably preserved that the sections cut from it permit detailed study under high powers and oil immersion (80). And the longer one studies mineralized or otherwise fossilized plants, the more is one impressed by the fact that the final results of study in the case of most florules very often depend far more on the persistence of the investigator than on uniformly good conservation. The restoration of ancient structures must at best depend upon the study of many specimens continued through a long period of years, and the best specimens are not always so much those which are strikingly conserved as those which after painstaking study are found to yield supplementary details of crucial structure.

Bearing such facts in mind, there appears to be little doubt that both the Maryland and Portland series will abundantly reward patient study. That these two longest-known series should remain to this hour the least-studied members of the Cycadeoideæ is a rather anomalous fact in the development of paleobotany. Necessarily the successful study of any series must begin with the types, and peculiarly in the case of the cycads does it become necessary to turn to the types and study them first in order to make satisfactory headway; for there is exactly that form of specific and generic variation which is bound to lead to much

confusion if any other course is pursued. This general fact has been urged more than once in this volume, but can not be too strongly emphasized. It is doubly true in the case of the Maryland trunks. Every specimen which has been called a type should be sawed through longitudinally, and then a selected half should be cut transversely and the resultant surfaces polished. Only thus can those lesser areas of finely conserved tissues be located and the best portions of the armor be blocked out to advantage for the supplementary leaf-base and fruit sections. Finally, when the types have been studied, one may determine with a very fair degree of precision those cotypes worthy of similar further study.

FIG. 8.—*Cycadeoidea marylandica* (Font.) Cap. & Solms. ×0.2 or less.

Latero-basal view of trunk and accompanying coniferous wood from the Potomac formation of Maryland An original Tyson specimen, now No. 1 of the Johns Hopkins University collection. The leaf-base spirals are wholly undisturbed by secondary branches or fruits, comparison with the more mature type (Vol. I, Fig. 1) indicating that the full-size preceding fruit growth had just been reached. From one of the Tyson photographs of 1867 found among the notes of Professor Marsh.

It must be held important scientifically to determine the species of Maryland Cycadeoideas, provided that such study is begun and carried through to a successful conclusion in the rigidly scientific manner just outlined. The results may prove to have a partially negative value—that is, there may be but a single species among all the Maryland trunks. But this also would be an interesting fact once definitely determined, since the Black Hills cycads include such a striking assemblage of species.

So far as mascroscopic features go, it must be frankly admitted that it is difficult to discern a second clearly marked species. All the Maryland trunks appear to form a continuous and homogeneous series representing a robust columnar form very distinctly inclined to the culminant or monocarpic type of fructification. For a time it seemed that two specific series could be distinguished, namely, a more or less microphyllous series embracing the original *Cycadeoidea marylandica* (1889) and *C. Tysoniana, McGeeana,* and *Fontaineana* (1897) on the one hand, and on the other a somewhat megaphyllous series, including chiefly the large trunk *Cycadeoidea Goucheriana,* together with *C. Uhleri* and the well-represented *C. Bibbinsi* (1897). But the most careful attention fails to bring to light any crucial differences in these several forms. Neither from such sections as have been cut, nor from inspection of the original species, and much less from the descriptions of Fontaine and finally of Ward, has any clear evidence been obtained of a second species from the "Iron Ore Beds." The trunks have throughout about the same large pith, the same development of thin woody cylinder, thick cortex, and heavy armor, with the same subrhombic to triangular leaf-base section and fairly profuse ramentum that one might expect to find in the case of any well-represented fossil cycad species found in varying stages of growth and conservation. (Compare the characteristic trunk of Fig. 8 with trunks of Plates 1 and 2.)

As late as 1905 Ward added to the extreme end of his series the two additional species *Cycadeoidea Fisheræ* and *Clarkiana,* although there is no evidence that either of these types presents any final difference from *Cycadeoidea marylandica.* The type of *C. Clarkiana* has nearly all its armor eroded away, and the horseshoe-shaped leaf traces appear in regular spiral order at the outer periphery of the cortex in the most striking manner; but any of the large specimens similarly eroded would present these same features.

The type *Cycadeoidea Fisheræ* is a far more noteworthy specimen, with a heavy ramentum and unbroken regularity in the spiral succession of its leaf bases of regularly flattened triangular scar outline. The trunk was evidently approaching a period of culminant fructification, as a close study of the surface reveals minute bract areoles in the axils of quite all the leaf bases. Such a trunk strongly suggests the marvelous Hermosa specimen *Cycadeoidea Dartoni.* But after all, the evident droop of the armor may be mainly responsible for the flattening of the upper surface of the leaf-base cavities, and had the trunk continued to grow it might not have matured more of its fruits than *Cycadeoidea marylandica;* or the latter type might perchance have been a somewhat sparsely fruited individual. However, nothing short of the adequate sectioning of the types above indicated can settle these doubtful points. Hence it is necessary to note and retain the order in which the Maryland species have been established. Fortunately, in all publications relating to them, the same sequence has been rightly followed, and it would be highly desirable to section and study the original types in this exact order.

1889: (1) *Cycadeoidea marylandica.*
1897: (2) *Cycadeoidea Tysoniana,* (3) *C. McGeeana,* (4) *C. Fontaineana,* (5) *C. Goucheriana,* (6) *C. Uhleri,* (7) *C. Bibbinsi.*
1905: (8) *Cycadeoidea Fisheræ,* (9) *C. Clarkiana.*

These so-called types are distributed as follows:

(1) *Cycadeoidea marylandica* (Fontaine), Johns Hopkins University, Baltimore.
(6) *Cycadeoidea Uhleri,* Museum of the Maryland Academy of Natural Sciences, Baltimore.
(2) *Cycadeoidea Tysoniana,* (3) *C. McGeeana,* (4) *C. Fontaineana,* (5) *C. Goucheriana,* (7) *C. Bibbinsi,* (8) *C. Fisheræ,* (9) *C. Clarkiana,* are with various cotypes in the museum of the Woman's College of Baltimore. The head types are numbered 1472, 1471, 1467, 1479, 1427, 6345, and 9050, respectively.

The order in which any future study of the Maryland cycads might best be arranged being so obviously the chronologic one, and there being so much doubt as to the precise value of macroscopic determination of species, it is not necessary to add any further specific diagnoses. Especially is this so since Berry has recently given, in a conveniently condensed form, the descriptions which supposedly delimit the several proposed types, together with at least one excellent illustration of each (*Cf.* Report of the Maryland Geological Survey, Lower Cretaceous, 1911, pp. 313–331, Plates XLII–L). These so-called specific descriptions are simply the catalogue list of specimens varying in conservation and growth stages. They could be added to indefinitely. It is, accordingly, sufficient for the present to subjoin the synonymy of the Maryland Cycadeoideas. With respect to their geologic age the opinion of Berry has been given as follows, in discussing *Cycadeoidea marylandica:*

"* * * The exact geological horizon in the Potomac Group has not been established with certainty for any except this one trunk, and for this reason the localities will not be given for the other species. Since the specimens do not occur *in situ*, the point where they eroded out or were plowed up has little significance, as they all come from the same circumscribed belt. It is quite possible that they are all of Patuxent age, and may have been reworked in later, even Pleistocene, deposits. The exact age of the trunks is of little biologic significance, since frond impressions are present throughout the various formations of the Potomac Group, the absence of petrified trunks being due entirely to physical conditions of deposition."

SYNONYMY OF THE CYCADEOIDEA SPECIES FROM THE POTOMAC GROUP OF MARYLAND.

(1) Cycadeoidea marylandica (Fontaine) Capellini et Solms-Laubach.

1860. *Cycas* sp., Tyson. First Report State Agric. Chemist, Maryland, p. 42.
1870. *Bennettites* sp., Carruthers. Trans. Linn. Soc., London, Vol. XXVI, p. 708.
1879. *Cycadeoidea* sp., Fontaine. Am. Jour. Sci., 3d ser., Vol. XVII, p. 157.
1890. *Tysonia marylandica*, Fontaine. Mon. U. S. Geol. Surv., Vol. XV, p. 193, Pls. CLXXIV–CLXXX.
1892. *Cycadeoidea marylandica*, Capellini and Solms. Mém. Real Accad. Sci. Inst., Bologna, Ser. V, Vol. II, pp. 179, 180, 186.
1897. *Cycadeoidea marylandica*, Ward. Proc. Biol. Soc. Washington, Vol. XI, p. 9.
1906. *Cycadeoidea marylandica*, Ward. Mon. U. S. Geol. Surv. XLVIII, 1905, p. 416, Pls. LXXXI, LXXXII, LXXXIII, Figs. 1, 2, 4; Pl. LXXXIV, Figs. 1, 2; Pl. LXXXVII, Figs. II, 3, 5, 6, 7; III, 1, 4; IV, 4, 5, 12–14; V, 2, 3, 5–7, 17; Pl. LXXXVIII, Pl. LXXXIX, Figs. II, 3, 4, 7; III, 2, 5, 8, 90, 91, 92.
1906. *Cycadeoidea marylandica*, Wieland. American Fossil Cycads, Vol. I, Fig. 1.
1909. *Cycadeoidea marylandica*, Scott. Fossil Botany, Fig. 199.
1911. *Cycadeoidea marylandica*, Berry. Maryland Geol. Surv., L. Cret., pp. 320–323, Pl. XLII.

(2) Cycadeoidea Tysoniana Ward.

1897. *Cycadeoidea Tysoniana*, Ward. Proc. Biol. Soc. Washington, Vol. XI, p. 11.
1906. *Cycadeoidea Tysoniana*, Ward. Mon. U. S. Geol. Surv. XLVIII, p. 432, Pl. LXXXVII, Figs. 1, 5; V, 4, Pl. XCIII.
1911. *Cycadeoidea Tysoniana*, Berry. Maryland Geol. Surv., L. Cret., p. 323, Pl. XLIII.

(3) Cycadeoidea McGeeana Ward.

1897. *Cycadeoidea McGeeana*, Ward. Proc. Biol. Soc. Washington, Vol. XI, p. 12.
1906. *Cycadeoidea McGeeana*, Ward. Mon. U. S. Geol. Surv. XLVIII, p. 434; Pl. LXXXVII, Figs. III, 3, 10 IV, 15; V, 8, 9, 19, 20; Pl. LXXXIX, Figs. II, 1, 8; III, 4, 9, 10; Pl. XCIV.
1911. *Cycadeoidea McGeeana*, Berry. Maryland Geol. Surv., L. Cret., pp. 323–324, Pl. XLIV.

(4) Cycadeoidea Fontaineana Ward.

1897. *Cycadeoidea Fontaineana*, Ward. Proc. Biol. Soc. Washington, Vol. XI, p. 13.
1906. *Cycadeoidea Fontaineana*, Ward. Mon. U. S. Geol. Surv. XLVIII, p. 439, Pl. LXXXVI; Pl. LXXXVII, Figs. I, 1; III, 2, 6, 8; IV, 1, 7, 9; V, 1, 10, 11, 13, 14, 16, 18, 21; Pl. LXXXIX, Figs. I, 1; III, 1, 3, 6, 7, 11; Pl. XCV; Pl. XCIV; Pl. XCVII; Pl. XCVIII.
1911. *Cycadeoidea Fontaineana*, Berry. Maryland Geol. Surv., L. Cret., pp. 324–325, Pl. XLV.

(5) Cycadeoidea Goucheriana Ward.

1897. *Cycadeoidea Goucheriana*, Ward. Proc. Biol. Soc. Washington, Vol. XI, p. 14.
1906. *Cycadeoidea Goucheriana*, Ward. Mon. U. S. Geol. Surv. XLVIII, p. 451, Pl. LXXXVII, Fig. I, 3; Pl. LXXXIX; Pl. XCIX.
1906. *Cycadeoidea Goucheriana*, Wieland. American Fossil Cycads, Vol. I, Fig. 7.
1911. *Cycadeoidea Goucheriana*, Berry. Maryland Geol. Surv., L. Cret., pp. 325–326, Pl. XLVI.

(6) Cycadeoidea Uhleri Ward.

1897. *Cycadeoidea Uhleri*, Ward. Proc. Biol. Soc. Washington, Vol. XI, p. 14.
1906. *Cycadeoidea Uhleri*, Ward. Mon. U. S. Geol. Surv. XLVIII, p. 454, Pl. LXXXVII, Fig. IV, 10; Pl. C.
1911. *Cycadeoidea Uhleri*, Berry. Maryland Geol. Surv., L. Cret., pp. 326–327, Pl. XLVII.

(7) Cycadeoidea Bibbinsi Ward.

1897. *Cycadeoidea Bibbinsi*, Ward. Proc. Biol. Soc. Washington, Vol. XI, p. 15.
1906. *Cycadeoidea Bibbinsi*, Ward. Mon. U. S. Geol. Surv. XLVIII, 1905, p. 456, Pl. LXXXIII, Fig. 3; Pl. LXXXIV, Fig. 3; Pl. LXXXV; Pl. LXXXVII, Figs. I, 2, 4, 6, 7; II, 1, 2, 4, 8, 9, 10, 11; III, 5, 7; IV, 2, 3, 6, 8, 11; V, 12, 15; Pl. LXXXIX, Figs. I, 5; II, 2, 5, 6; Pl. CI–CIV.
1911. *Cycadeoidea Bibbinsi*, Berry. Maryland Geol. Surv., L. Cret., pp. 327–328, Pl. XLVIII.

(8) Cycadeoidea Fisheræ Ward.

1906. *Cycadeoidea Fisheræ*, Ward. Mon. U. S. Geol. Surv. XLVIII, p. 470, Pl. LXXXVII, Fig. III, 9; Pl. CV.
1911. *Cycadeoidea Fisheræ*, Berry. Maryland Geol. Surv., L. Cret., pp. 329–331, Pl. L.

(9) Cycadeoidea Clarkiana Ward.

1906. *Cycadeoidea Clarkiana*, Ward. Mon. U. S. Geol. Surv. XLVIII, p. 472, Pl. LXXXIX, Figs. I, 2, 4; Pl. CVI.
1911. *Cycadeoidea Clarkiana*, Berry. Maryland Geol. Surv., L. Cret., pp. 328–329, Pl. XLIX.

FIG. 8*a*.—Dakota-Lakota sandstones in Cañon of the Fall River below Hot Springs, South Dakota, looking south. Section of the Black Hills "Rim" or escarpment bordering the Red Valley or "Race Course" of the Trias.

The Morrison shale with the lower Cycad horizon is absent in this southeast sector of the "Rim." The upper cycad horizon of Lakota sandstones and shales outcrops at the side and base of the cañon. The *Cycadeoidea excelsa* came from near this point. (*Cf.* Figs. 1*a* and 14*a*.) Photographed by N. H. Darton.

CHAPTER V.

PIEDMONT-BLACK HAWK SERIES.

The Cycad Valley of the Piedmont-Black Hawk segment of the Black Hills "rim," illustrated on Plates XLVIII–L of Volume I, is one of the best-known and most distinctive of all American cycad localities. This locality is striking from the scenic point of view and interesting because of clearness of stratigraphic relations. It was the first portion of the Lower Cretaceous cycad-yielding girdle of the Black Hills in which petrified specimens were collected. Though Professor Ward did not give his preliminary note on the tall Black Hawk species *C. Jenneyana* until a year after Macbride had described the typical Minnekahta species *Cycadeoidea dacotensis*, the former and certain associated specimens had been collected far earlier than the Macbride types.

Aside from early discovery, however, the Piedmont-Black Hawk series of cycads has great intrinsic interest due to the fact that a closely related but finely differentiated series of species is represented. Though by no means so perfectly silicified, or rather stained, as various other forms, this group must long remain one of the clear points of attack in any effort to discern distinct species of American fossil cycads; it is also notable because of the discovery of the true character of both fruit and foliage in the Cycadeoideans in the great trunk *Cycadeoidea ingens*. Moreover, because all of the 300 specimens collected from about the Cycad Valley represent columnar types only, including about a half dozen distinct species, much sharper comparisons with the previously known series from Maryland and from Europe can be drawn than in the case of the Minnekahta series, which includes so many branching forms. Such, though having essentially the same features of trunk and floral structures as the earlier described columnar trunks, are not only the most complex members of the Cycadeoideæ, but are the most difficult to determine specifically because the separate branches are so often broken apart.

Another fact which goes far to make up for the lack of well-differentiated histologic structure in most of the Black Hawk cycads is the striking color differentiation which marks out all larger organs as the result of the particular type of chalcedonization. This, while distinctly characteristic for the group and scarcely duplicated in any other trunk series, varies much in the different specimens, the polished surfaces of which are often notably beautiful. While in some specimens the color of the quartz is gray and subdued, there are very few in which all outlines of larger features fail of distinctness, and in most of the specimens the pith, wood zones, cortex, leaf bases, and fruits have a variation of color and clearness of contour in strong contrast to the more or less vague outlines on the darker polished surfaces of some of the far more wonderfully silicified Minnekahta specimens. Within restricted limits advantage has already been taken of the very striking character of the polished surfaces yielded by these trunks. As the plates show, a handsome series of transverse trunk sections is already at hand, besides a number of tangential sections through the armor. In fact, quite the only lack is that of longitudinal trunk sections, difficult and costly to cut.

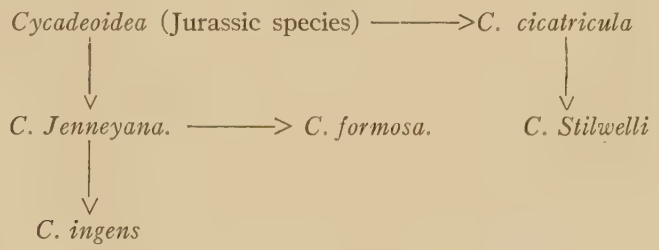
Furthermore, the much-fractured character of many of the Cycad Valley specimens is not in the end a great disadvantage to their study; in fact, the seemingly great number of

fragments is partly due to the presence of at least one unusually tall species, *Cycadeoidea Jenneyana*, which was more liable to fracture than short and more or less spherical forms. Yet these fragments are mostly found to be valuable specimens which usually show their main features very clearly; sometimes details are plainly present that in the case of the completer trunks can only be observed after sectioning. However, the series taken as a whole includes some of the most sightly specimens known, and it must be held peculiarly fortunate that the Piedmont-Black Hawk series can be seen so nearly in its original entirety in the Yale collections. These include all but a very few of the trunks ever recovered and all the primary types save *Cycadeoidea Jenneyana.*

The fact that nearly all of the Black Hawk cycads have been brought together and conserved in a nearly intact collection causes the compactness of the group of closely related species to stand out the more remarkably. Plate 4, which illustrates but a part of the Yale collection, shows clearly the transition from low-growing trunks to the largest and tallest known. And most interesting is the series of wood cylinder types, passing all the way from the thinnest to those with the heaviest wood development ever observed in the Cycadeoideæ.

This group was believed by Professor Ward to include no less than seven species, but it is barely possible that ultimate and searching examination of the finer structure may eliminate two of these and divide the remaining five indubitably distinct forms into a group of two smaller and three larger species. Externally the series appears nearly continuous, but when all the features of form and structure are considered, the five species are found to be readily recognizable from quite unmistakable features. As will be seen from the more detailed descriptions given below, these species range themselves according to their average mature size, beginning with the smallest, thus: (1) *Cycadeoidea cicatricula;* (2) *C. Stilwelli;* (3) *C. formosa;* (4) *C. Jenneyana;* (5) *C. ingens.*

This series, apparently a very local hill-side rather than a low-ground group of plants, may thus be tabulated as genetically derived from several rather more primitive Jurassic species, likewise simple-stemmed and with a fairly copious ramentum:



Before considering these species more closely, it may be useful to give a simple introductory account of the group as a whole. This is desirable because there can not be finality in treating these species, as already clearly explained in the introductory chapters, although the original descriptions must be kept in view.

It is preferable to consider these Piedmont-Black Hawk species as derived from two or more rather than a single species, because of the single feature of leaf-base bundle distribution, which is of the simpler marginally aligned pattern in the two species *Cycadeoidea Stilwelli* and *cicatricula* and of the distributed or somewhat *Encephalartos*-like form in the other three species. As yet no generic hiatus between the aligned and the distributed types of bundle pattern has been detected, distinct as they may appear at first sight, and notwithstanding the fact that distributed bundles are a quite uniform feature of all the existing species of *Encephalartos.*

Cycadeoidea cicatricula is noted for a general absence of fructification, and suggests most strikingly a Russian form *Cycadeoidea (Tubicaulis) rhomboidalis*, of which I have seen a model in the Paris Museum; but of course such comparisons are of little value. I can not say what *Tubicaulis* really is and the cicatriculas may be merely young trunks.

The other three Black Hawk species form a closed group, with *Cycadeoidea Jenneyana* possibly the more primitive because of its abundant ramentum and leaf bases of moderate size. From it both the other species which have pauciform ramentum may have been derived. Of these *C. ingens* is sometimes very hard to separate from its tall relative. Even on the type (Trunk 100 of the Yale Collection) one may see leaf bases of most variable size with forms not outwardly distinguishable from those of *C. Jenneyana;* but careful attention shows the presence of a series of trunks with enormous leaf bases, often quite 5 cm. in lateral by 3 cm. in vertical diameter.

Moreover, this series contains young trunks as well, so that we know that even the juvenile *C. ingens* was often characterized by a great spread of fronds, very comparable to those of *Cycadeoidea megalophylla*. On the other hand, the tall trunks referred to *C. Jenneyana* are likewise distinguishable as a series, though consonant with a freer production of ramentum the leaf-base patterns are of medium size and very variable form, which has possibly led to the erection of several superfluous or doubtful species like *C. occidentalis*.

Here one might incline to place that English trunk *Cycadeoidea gigantea* of Seward, which has many features in common with *C. Jenneyana* and none different, that I know of. Our American species has been more studied and, though not figured until 1899, it was preliminarily named in 1894, nearly three years earlier than the great British Museum specimen from the "dirt bed" of the Isle of Portland.

The single trunk referred to *C. formosa* is just emerging from the *pulcherrima* stage, and being a comparatively young or else flattened spherical type, it is too small to be regarded as an aberrant form of either *C. ingens* or *C. Jenneyana*. In outer features, especially in general form and size of the trunk and leaf bases, this trunk suggests the Isle of Wight *Bennettites Gibsonianus*, and may even agree in its fructifications, which are of medium size, but poorly preserved. The chief differences from the latter are paucity of ramentum and departure from the simpler bundle pattern. Furthermore, this trunk has, in proportion to its size, a far thinner woody cylinder than any of the other Black Hawk forms. This feature alone serves to distinguish it.

As already indicated, the Cycad Valley trunks more especially resemble foreign specimens. To the other American series of unbranched trunks there is no very marked specific resemblance, so far as has been learned. In the Wyoming series of small trunks, which is older, the bundle patterns are different, and the ramentum for the greater part more profuse. The single trunk from Boulder (Colorado) is of different bundle pattern, though decidedly columnar; and the non-branched and low-growing robust forms from Maryland appear to be rather more closely related to the much-branched Minnekahta series. One does not then discover that a single Cycad Valley species appears with certainty in any other American locality. This suggestive fact merits a brief interpretation before passing to the more detailed notice of these Cycad Valley species. It may be pointed out that any such structural differences, as tendency to reduced ramentum and the markedly columnar form, may have a certain ecologic significance. The great number of branching forms found in beds of identically the same age at Minnekahta may have come from surroundings markedly different from those in which grew the columnar Black Hawk forms. There are far more conifer trunks in the Piedmont region than at Minnekahta; whence it is likely that the columnar

cycads of the Cycad Valley were brought forward at flood time from some remoter upland cycad florule, where they grew in more or less open reaches and dells of great *Araucaria* forests; whereas the branched cycad types of Minnekahta may have been derived from more distinctly littoral, lake-front, or delta regions, in some instances being covered over near where they grew. But this is only a tentative suggestion. I am not aware that the Portland "dirt bed" has ever been considered as representing other than a fertile low plain, on which grew the cycads, the numerous associated stumps of large coniferous trees, and occasional logs (*Araucarioxylon antediluvianum*) in the very place where now found silted over; and while the few conifers represent moderately large trees, the far more abundant Cycadeoideas, are mostly small and spherical or at least low-growing species, though including the great columnar *Cycadeoidea gigantea*.

Cycadeoidea Jenneyana Ward.

1894. WARD. Proc. Biol. Soc. Washington, Vol. IX, p. 87.
1898. WARD. Proc. U. S. Nat. Mus., Vol. XXI (No. 1141), pp. 216–221.
1899. WARD. Ann. Rep. U. S. Geol. Surv., XIX, pp. 627–632, Pls. CXXI–CXXXII.
1900. WARD. Am. Jour. Sci., Vol. X, Nov., p. 332 (enumeration of catalogue numbers in Yale Collection).
1906. WIELAND. American Fossil Cycads, Vol. I; various notes on occurrence, form, and structure in text, with figure of a heavy wood cylinder, Pl. XIV, photograph 1 (*cf.* pp. 78–80, 131, 132, and Fig. 65).

Any description or consideration of *Cycadeoidea Jenneyana* must, not alone for reasons of convenience, but of strictest priority as well, begin with the original U. S. National Museum type briefly mentioned and named by Professor Ward in 1894; for it is to be recalled that at that time the only cycad trunks described from America were: first, the small and beautiful trunk called by Lesquereux *Zamiostrobus mirabilis* in 1876, and hence the earliest described of all American silicified cycads; second, *C. marylandica*, or *Tysonia marylandica* of Fontaine 1889, a low-growing and robust but columnar trunk; third, that very different, low-growing, and branching form, *C. dacotensis*, of Minnekahta, the latter antedating the present form but a single year. The smaller species of Italian trunks, so much like the Maryland forms, were described in considerable variety by Capellini and Solms some two years earlier, while the very similar English forms were all known, save *C. gigantea* Seward, which of all European cycads is nearest to *C. Jenneyana*, but was not described till five years later. The only other European trunk which can be mentioned in this connection is *C. Reichenbachiana*. It had the same habitus as Ward's type, and it shows that same non-tapering, strictly columnar form, with leaf bases of moderate rather than of gigantic size, and the same laterally borne, short-peduncled fructifications. But, as I was able to determine when at Dresden, aside from various minor differences, the flowers of *C. Reichenbachiana* had 16 microsporophylls, while those of *C. Jenneyana* never have more than 12. It is accordingly clear that not only is *Cycadeoidea Jenneyana* specifically distinct from all of the European trunks, but that, along with *C. marylandica* and that other Black Hills specimen *C. dacotensis*, it is one of the initial and indubitably valid species. The type is distinct; its priority can never be questioned; and with its principal macroscopic characters already outlined in nicety of detail by Professor Ward, it now remains to define the species more closely and thus set the specific boundaries on the basis of a great number of trunks and the completer knowledge they afford. For thus may we most conveniently determine how far it is at present possible to judge whether the next related forms, namely, the tall *C. excelsa* and *C. gigantea* on the one hand, and the robust *C. ingens* on the other, are valid species or merely synonyms of *C. Jenneyana*.

The first of these questions may best be initially discussed by giving the following résumé:

C. Jenneyana.	*C. excelsa.*
(1) Trunks large and tall, up to 130 cm. high.	Same.
(2) 30 to 40 cm. in diameter.	112 cm. in circumference (but worn).
(3) (Summit tapering in two of three forms known.)	The same. Has "an enlarged base."
(4) Organs of armor horizontal.	Same.
(5) Scars subrhombic to triangular with mostly rounded angles, sometimes kite-shaped.	Scars imperfectly rhombic (but rather regular because showing at a lower level; at base, rounded, kite-shaped, etc.).
(6) Left-right leaf base spiral 40° to vertical axis. Right-left spiral 60°.	Left-right spirals 20° to 40°. Right-left spirals 50° to 60°.
(7) Leaf-base scars 20–30 mm. wide and 12–25 mm. high.	Leaf-scar diagonals 16 to 25 mm., but leaf bases conserved only through length of some 2 cm.
(8) Leaf-base bundles scattered and forming imperfect marginal row.	(The same in *C. gigantea* and doubtless here also.)
(9) Ramentum interspaces filled but variable, thick.	The same wherever the armor is all present, but normally sparse near insertion of leaf bases on cortex.
(10) Fructifications numerous, large, and well developed, 25 to 40 mm. in horizontal and 18 to 26 mm. in vertical diameter.	Fructifications numerous, a small series, also a large series lying in interrupted rows running in the same direction as the leaf bases which they crowd and thrust aside; from 25 to 38 mm. in diameter.
(11) Armor 8 to 9 cm. thick.	4 to 7 cm. thick (trunk much worn).
(12) Liber zone indistinct, narrow.	Liber zone, 2 cm. thick (narrow).
(13) Wood 2 cm. thick, without visible subdivision into rings. (Altitude of measurement on trunk not given.)	Wood 2 cm. thick, not divided into "3 rings." The xylem only slightly exceeds the phloem in thickness. (But see Pl. 43 for a comparison.)
(14) Medulla 15 cm. in diameter.	Medulla 13 cm. in diameter.

From these parallel columns, which are mainly taken from Professor Ward's original description, with certain minor rectifications, it would seem possible that barring accidental features of silicification and subsequent erosion the so-called type *C. excelsa* is really no more than a variety of *C. Jenneyana* or identical with it, although a hasty decision must not be made. But when one institutes comparisons with *C. gigantea* of the Isle of Portland, much the same impression of marked similarity is gained, with the sole exception that the stage of fructification appears less advanced. However, a large tangential surface of *C. gigantea* has not been polished, although the flattened condition of this trunk would readily lend itself to such study. Doubtless such a section would disclose many young fruits, just as must prove the case in *C. excelsa*. (See table on page 89.)

The necessary data for a rigidly accurate comparison of these several types are thus lacking, and, as continually urged in the preliminary discussions of specific indices, it is far too early to begin "lumping" or uniting any of the species of silicified cycads; nor will the thin-section series greatly help matters for some time to come. Indeed, in my judgment, only that profounder knowledge of these marvelously conserved plants resulting from prolonged laboratory study and persistent collection of supplementary material can make it safe to propose any marked changes in specific names. It is perfectly feasible to make change after change in the nomenclature of leaf impressions or of isolated stems or fruits with structure conserved, where one may so largely depend on indices which are definite, all in full view, and unchanging in their value, and where, moreover, study is mainly based on

types as complete as it may ever be hoped to find; but here the case is entirely different, because of the wide-set limits of unusual conservation, which in the case of any of the forms more especially under consideration make it likely that entire new series of trunks, extending from mid-age to the period of culminant fructification, may at any time be recovered and reveal wholly unsuspected features. Figures 9 and 10 may be profitably studied in this connection.

Certainly my first impulse was to unite *C. excelsa* to *C. Jenneyana*, and indeed this was done in the first draft of this description. But after the later preparation of a larger though far from complete series of polished trunk sections I feel less competent to say that two distinct species are not present. The longer these studies have been continued, the more convinced have I become that the better course for the present is to avoid additions to or changes in the fairly long list of species and genera already proposed.

The armor sections of figures 9 and 10 afford some further structural details of interest. In particular they disclose the presence of numerous scale leaves. Figure 9, from Yale trunk 551, is the more tangential of the two.

FIG. 9.—*Cycadeoidea Jenneyana.*

Tracing from polished tangential surface traversing outer armor of Yale trunk 551. ×0.4.

As photographed on Plate 4, the large trunk segment 551 appears to bear numerous well-developed fruits; but the present section passes several centimeters beneath the surface of the armor and shows that the fruits are still very young. The bract envelopes, however, so thrust the leaves and numerous scale leaves out of their original position that the initial spirals are no longer determinable. In the polished area (fig. 9), about 40 cm. long by 20 wide, some 75 foliar bases appear, probably about equally divided

between leaves and scale leaves. The great irregularity of form, together with the vertical depth of the foliar bases and the enormous development of ramentum, serve to distinguish the segment from *C. ingens*, where scale-leaf bases are relatively few and ramentum less in quantity. Floral axes are one-third as numerous as the foliar bases and a few marked by arrows appear to have developed ovulate cones; but the tissues are too much chalcedonized to reveal the finer structural details.

The more deeply cut tangential surface of figure 10 displays the compacter grouping of the armor organs usual to sections passing near the outer cortex. The much-reduced outline drawing conveys but a scant idea of the handsome polished surface 35 by 20 cm. in area. Note the uniform shape of both the larger and lesser leaf bases, which are in the proportion of about 10 of the former to 1 of the latter. As these smaller bases, though irregularly interspersed among the larger forms, yet go to make up with these latter the two equal 60° spirals without a single member lacking or over, they are not adventitious. They are best explained as exemplifying a scale-leaf condition midway between that of the existing *Macrozamia spiralis* without scale leaves and *Cycas* with abundant scale leaves.

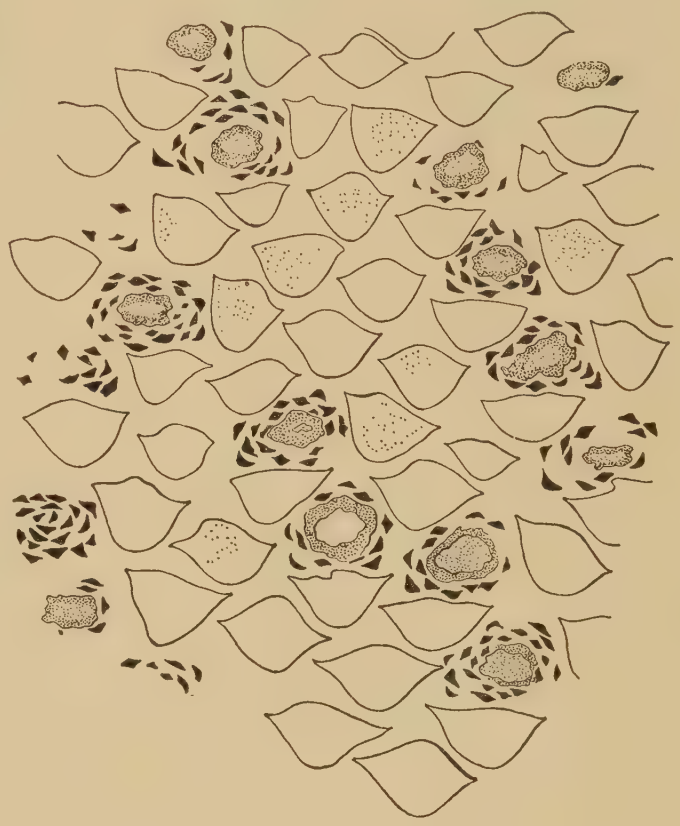


FIG. 10.—*Cycadeoidea Jenneyana* (?) $\times\frac{3}{7}$.

Tangential trunk section traversing mid-armor of a more or less nearly basal segment of a large trunk 4 to 6 cm. above the leaf and peduncle insertion on cortex, and passing through numerous bract-bearing peduncles. (Author's specimen.)

The leaf-base bundles are not very distinct on the original surface and do not at this level form a characteristic pattern. Enough are shown to make clear the kind of distribution.

The fruit axes, of which 17 are cut, have a distinct tendency to run in spirals, much as do the leaf bases to which they are axillary. Only two axes appear to be less advanced than the average. But this lesser size is due to the peripheral position where the barrel-shaped peduncles are cut more distally through the constricted portion just below the cone base. All the axes are therefore in a quite equal stage of growth. They are again one-third as numerous as the leaf bases, large and small. Compare with figure 27, Volume I, where the small leaf bases are more numerous, the area being perhaps nearer the trunk summit. That figure and the present figures 9 and 10 constitute the first definite information as to the occurrence and distribution of scale leaves in the Cycadeoideas. This subject is somewhat further amplified in the description of *Cycadeoidea Dartoni*. It may be incidentally observed that any marked tendency of

the scale leaves to occur in nodes or belts must be more or less obscured in such robust forms as *Cycadeoidea*. Alternant nodes of foliage and scale leaves could only appear with any degree of regularity in slender-stemmed relatives, as in *Williamsonia*.

FRUCTIFICATION OF CYCADEOIDEA JENNEYANA.

The fruits of the original type of *C. Jenneyana* still require study, but must be young, as the leaf-base spirals are distinct and but little disturbed. In consequence, we are not yet able to describe the true fruits of *C. Jenneyana*, the earliest-named of the Black Hills species, with the desired certainty. Longitudinal and transverse sections of the type trunk also fail, and such must be had before anyone can say with absolute precision that other trunks with more advanced fruits belong to the species *C. Jenneyana*. Meanwhile, in casting about among the Black Hawk specimens for trunks with the best-marked fruits, it was noted that the rather young trunk No. 115 of the Yale collection, which appears to be a *C. Jenneyana*, bore, in addition to various strobili sparsely scattered over its surface, two fruit axes of very unusual interest. These, as may be observed in Plate 6 (phot. 2), were situated in the mid-region of the trunk 15 cm. apart, the one plainly being in the staminate-disk stage and the other by far the largest ovulate cone at any time observed in Black Hawk specimens. Accordingly these fruits were drilled out of the trunk in the form of cores after the usual mode employed for closer study. This done, the staminate axis was cut transversely, first through its base, and then through the apex, after which the intervening segment was cut longitudinally. The ovulate cone was only cut once longitudinally. But as the histologic details were not found clear enough in either of the fruits to warrant the cutting of thin sections, study was continued from the carefully polished surfaces. These polished surfaces, however, proved to have, in both the ovulate and staminate fruit, a jaspery brilliance of coloring not surpassed and scarcely equaled by any sections or polished surfaces prepared during these entire studies. As shown in the drawings, all the larger features are clearly brought out, although it required most patient joint study of both author and artist to determine with certainty all of the details to be observed in the transverse section through the summit of the staminate axis. In particular the position of the rachides was not at first clear. But the drawing was carefully proved point by point until assured accuracy was reached.

Text figures 11 A–D clearly display the characters of these two handsome fruits. The bisporangiate axis (Fig. 11 A–C) has a disk of 13 fronds bearing large synangia which approach maturity. The cushion of the central cone is much elongated and ends in a more or less filamentous extension. The ovulate zone forms but the thinnest envelope of the cushion, and the individual organs are, as compared with the large synangia, so minute as to at once suggest an abortive condition.

The adjacent ovulate cone (Fig. 11 D) affords a strong contrast to the very immature cone of the bisporangiate bud because of its relatively mature condition. The seeds equal in size those of some other species with smaller cones where embryos are present; the mass of seed stems and interseminal scales is long and well developed. The parenchymatous cushion is of the flatly convex type, and it is important to observe that the hypogynous disk line of insertion (I) appears as if completely grown over. It is in fact very improbable that any earlier borne basal disk could have reached even a minor development. This is, moreover, the largest flat-disked cone yet found, also the largest observed in any columnar *Cycadeoidea*, falling but little short of the maximum size seen in the great branching species. The mature size in the latter has, however, not been determined.

In interpreting the bearing of these fruits on the question of monœcism in the Cycadeoideæ careful attention should be given to their position on the trunk. Observe that the isolated ovulate cone (D) and the bisporangiate axis (A–C) of figure 11 are indicated as fruits I, II, respectively, on Plate 6, photograph 2; also that a second bisporangiate axis (III) is present. Other axes are not readily determinable, fructification being scattering

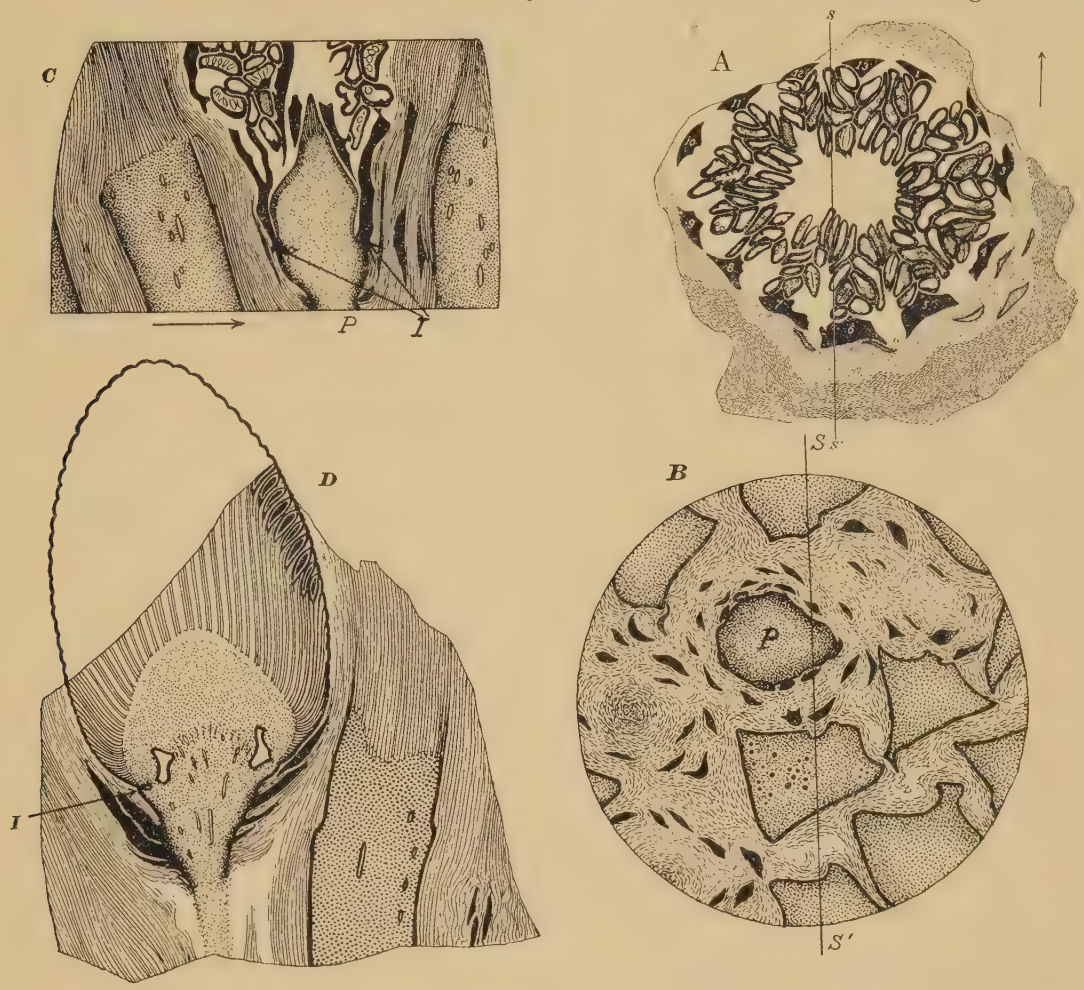


FIG. 11.—*Cycadeoidea Jenneyana.* Bisporangiate and ovulate fructifications cut from Trunk No. 115 of the Yale collection. (Piedmont-Black Hawk series.)

Drawings made directly from polished surfaces. All are natural size except A, which is enlarged to $\frac{5}{4}$. A–C, apical, basal, and corresponding longitudinal sections of bisporangiate flower bud, No. 11, photograph 2, plate 6; D, ovulate cone No. 1 of photograph 2, plate 6.

A. Transverse section through disk of 13 microsporophylls cut just above superior border of campanula.

B. Basal section through leaf bases surrounding peduncle (P) of flower seen in longitudinal section at C.

C. Longitudinal section of flower bud from base line of which was cut the transverse section B and from top line the transverse section A. The peduncle, adjacent leaf bases, and outline of the bract-inclosed strobilus plainly appear, also the disk inserted at the base (I) of the central ovulate cone of rather irregular but distinctly elongate form.

D. Longitudinal section through large ovulate fruit adjacent to the flower bud A–C. This section, except for slight obliquity at lowermost end of peduncle, cuts the fruit in the nearly median plane.

rather than abundant. Now, cones with nearly flat cushions have been seen in other species; and as the cushion of the bisporangiate bud is elongated, with the long ovulate axis abortive, while the cushion of the large ovulate cone is convex, one can scarcely escape the conviction that this is a clear case of Cycadeoidean monœcism. Shortly after these fruits had been cut, I had the pleasure of restudying the sections and reviewing the evidence afforded by them with the eminent evolutionist, Professor Hugo DeVries, on the occasion of his first

visit to Yale. After going over the sections with careful attention to all features as well as to the position of the fruits on the trunk, Professor DeVries felt that the evidence for the monœcious condition was wholly conclusive. This, however, is the only example in the Cycadeoideæ where monœcism is directly indicated. The flowers of *Cycadeoidea dacotensis* were at first thought to be monœcious, but all later study has seemed to indicate that they were mainly if not always bisporangiate; while in the case of other species, like *C. Wielandi* discussed elsewhere, the evidence for a monœcious habit is not as yet entirely conclusive.

Notwithstanding the large number of *C. Jenneyana* trunks with fruits more or less advanced in growth, the evidence for monœcism must for the present doubtless rest as here given. Only a few staminate flowers of apparently the same species as the present have been encountered from time to time, though these have in all cases shown the elongate type of cushion with markedly immature and minute seed zone and 10 to 13 fronds. That no more of the large ovulate cones have been seen on other trunks may be due to chances of conservation as well as fortune in observation; with so many specimens at hand, it seems strange that the two striking examples here illustrated should remain quite isolated.

Cycadeoidea ingens Ward.

1898. WARD. Proc. U. S. Nat. Mus., Vol. XXI, No. 1141, p. 221.
1899. WIELAND. Am. Jour. Sci., 4th ser., Vol. VII, No. 39, pp. 219–226, Pl. II–IV, with 2 figures in text. (Figures type trunk and its microsporangiate fructification, this being the first discovery of staminate organs in the Cycadeoideæ.)
1899. WIELAND. Am. Jour. Sci., 4th ser., Vol. VII, pp. 305–308, with Pl. VII. (Describes prefoliation and structure of leaves of type, being first description of these structures in any silicified trunk.)
1899. WARD. Ann. Rep. U. S. Geol. Surv., XIX, pp. 632–633. Pls. CXXXIII–CXLIII. (Figures type and various other specimens.)
1900. WARD. Am. Jour. Sci., 4th ser., Vol. X, p. 332. (Refers various additional Cycad Valley specimens to this species.)
1900. SCOTT. Studies in Fossil Botany, pp. 466–468.
1901. WIELAND. Am. Jour. Sci., 4th ser., Vol. XI, p. 423.
1906. WIELAND. American Fossil Cycads, Vol. I, Pls. I–IV–A; and text-figs. 19, 44, 45, 49, 51, 54; also figures on pages 260 and 261. (These figures of *C. ingens* are all based on the type and quite fully reveal its form and structure. Supplementary sections of young leaves from another specimen are given on plate 19, photographs 1, 2, 3, 6, 7, 8; also, the locality of the type and important associated specimens is shown on Plates XLVIII–L.)
1914. WIELAND. Am. Jour. Sci., Nov., p. 454. (Figures stomata of young leaves.)

Cycadeoidea ingens is the grandest species included in the genus *Cycadeoidea*. Other trunks may have been handsomer because of their branching habit, while both the Isle of Portland and Piedmont-Black Hawk localities yield slightly taller trunks, and from Minnekahta comes the great trunk called by Ward *Cycadeoidea colossalis*, which vies in size; but no other species had nearly so great a spread of fronds or so well illustrates the simple columnar trunk with a huge foliar crown and large flowers; also, both flowers and leaves are of much historic interest as the first of their kind to be sectioned and studied in the Cycadeoideæ.

All the specimens of *Cycadeoidea ingens* are from the Cycad Valley and are included in the great Yale collections. Those which are regarded as fully illustrating the species are the type which reveals, as above annotated, all the chief characters of the mature trunk with its foliage and flowers, and the base No. 117, together with a wedge, 614. The latter display leaf base and stem structure better than the type. Nor is it necessary to minutely repeat the descriptions of these features as already given in much detail in Volume I. It should be recalled that the base No. 117, although of only medium size, has enormous leaf bases, while the nearly complete longitudinal half No. 614 shows the simple heavy wood zone.

From these various specimens *Cycadeoidea ingens* is indicated as a series of heavy silicified or chalcedonized trunks, never quite reaching 1 m. in height, as do *C. Jenneyana* and

C. excelsa, but attaining fully 60 cm. in diameter and weighing up to 300 kg. The frond bases are of fairly constant large size, and from 35 to 50 mm. in vertical thickness; the medulla is of moderately large size; the xylem cylinder is composed of compacted and extraordinarily heavy woody wedges; the collateral bundles are narrow, but as much as 4 cm. thick, the tangential width being only 1 cm., with a xylem depth of 2.5 cm. to 1.5 of phloem; the cortex is thin; the erectly prefoliate leaves appeared in closely serial order, with nearly equal rate of rachidal and pinnule growth; the flowers are moderately numerous or sparse in number, and probably did not appear until the parent trunk reached large size; the young seed cones are distinctly conical, with 12 or 14 surrounding staminate fronds, the mature ovulate cones being as yet unknown.

These are the main larger features of *Cycadeoidea ingens*, but a clear picture of this species can only be had after very carefully reading the descriptions of the associated Black Hawk cycads, especially *C. Jenneyana*. Among the hidden characters of the great type of *C. ingens* about which one would most wish to know are, first of all, the dimensions of the woody cylinder and the medulla. But necessarily, in the presence of so much material of far better histologic conservation and often equal interest, it is easy to see that there are other reasons than merely the formidable size of this type which may long or perhaps always prevent sawing it through longitudinally and transversely. Certainly it would be highly desirable to know definitely just what has been the increase in thickness of the woody cylinder with age; but with the type remaining uncut and a similarly gigantic specimen as yet unknown, one can only surmise as to the extent of secondary wood growth from such fragmentary large trunks or lesser and far younger specimens as have been cut. Reference to the excellent plates 8 and 9, also Plate XIV, Volume I, showing large, polished trunk sections, will enable anyone to comprehend the possibilities of woody-cylinder thickening toward the trunk base and the zone of root insertion, where, for at least a short distance, the wood must close in to form a nearly solid stem much resembling *Cordaites*.

FIG. 12.—*Cycadeoidea ingens.* ×0.4.

Aside from mention of the above trunks, we are not as yet in a position to make much of an incursion into the *Cycadeoidea ingens* borderland on the only sound basis—that of polished surfaces and thin sections. Trunk No. 91 of the Yale collection has, however, been made the subject of interesting study, despite its much chalcedonized texture. A large transverse armor section of this trunk segment has been polished down, as shown in figure 12. The figure shows a sharply reduced tracing made directly from the tangential polished surface traversing the outer armor. This surface is 46 cm. long by 16 wide, and the largest that could be had without cutting so deeply into the armor as to produce marked change in the leaf-base sections, varying from the normal sections at the center of the area to very obliquely cut bases at the periphery. As Plate 4 shows, specimen 91 is the upper segment of a tall trunk terminating in a large and fine apical bud which evidently conceals a young leaf series. The smaller bases of this long armor section must pertain to scale leaves, and the presence of a few young adventitious fronds or scales is also indicated. Young fruits are present in proportion to the leaf bases about as 1 to 4. Only one of the fruits, an ovulate cone *O. S.*, has reached appreciable size. All the others are very young, although the bract groups already thrust most of the leaf bases out of the earlier spiral alignment. The condition seen may be a younger stage of the monœcious development just described in *C. Jenneyana*. One might well expect to find in the monœcious forms just such young ovulate cones as that at *O. S.* accompanied by still younger axes, mostly staminate.

Professor Ward thought it most consistent to include trunk No. 91 in *C. Jenneyana*, appending a question mark; yet if he had seen such a large tangential section through the armor as that figured, a reference to *Cycadeoidea ingens* would almost certainly have been made. In outer form there is a certain resemblance to *C. Jenneyana*, and it must be admitted that the medulla is rather small and the woody cylinder rather thin for inclusion in *C. ingens*, as now provisionally suggested, because of the great size of the leaf bases.

FIG. 13.—*Cycadeoidea ingens* (?). Yale trunk No. 642. Transverse section of leaf base. Natural size.

Other trunks which may receive mention here, although of still more uncertain specific position, are the Yale specimens 642 and 656, noted as follows:

No. 642, a Black Hawk specimen, as illustrated on Plate 6, photograph 4, should receive mention under the present specific heading, although it may yet prove to be of a new and undescribed species, since the leaf bases show the aligned bundle pattern much nearer the cortex than has been noted in other *C. ingens* trunks. No. 642 is an incomplete basal segment 25 cm. in height, indicating a trunk as large as *Cycadeoidea ingens* type. As shown in figure 13, the leaf-base-bundle pattern of the mid-zone of the armor suggests a different species from any of the other Black Hawk specimens, in which all the forms with large leaf bases have the distributed instead of the aligned bundle pattern throughout the lower armor region. The young fronds of *C. ingens* type of course show alignment of bundles well out on the petioles. (*Cf.* Vol. I, Fig. 33, 9–12.)

While this specimen is too much chalcedonized to yield clear microscopic characters, there can be no mistake about the bundle pattern, and the U-bundles, even among the Black Hawk specimens, are conspicuous for their large size. The cavities left by imperfectly conserved peduncles may be noted in photograph 4, Plate 6. The medulla exhibits above a very remarkable fully eroded, cone-in-cone structure, not wholly corresponding with the axis of the plant, and also plainly appearing in the illustration. These medullar cones

are not essentially different from those observable in the polished transverse section of the trunk illustrated on Plate 9, but are of some interest as the largest examples of their kind wholly eroded and fractured out.

The armor is too much worn down to permit measurement of the leaf bases, which were large, as large as those of *C. Jenneyana* or *ingens*. But other dimensions which have value in trunk comparison are:

Yale trunk No. 642.	Base.	Top.
	cm.	*cm.*
Medulla (diameter).....	15	20
Wood (thickness).....	7	3
Cortex (thickness).....	7	7

Another very interesting basal trunk segment, No. 656 of the Yale collection, illustrated in transverse section on Plate 5, photographs 5, 6, and in tangential armor section in the adjacent text-figure 14, may conveniently be here considered. This trunk segment has the same U-bundle pattern as No. 642, but a far heavier wood zone, which prevents reference to one and the same species. The two trunks in question may belong to the same section of their genus, though all that can now be done is to feature them as characteristic Piedmont-Black Hawk stems awaiting completer knowledge of the wood zones of the several types.

FIG. 14.—*Cycadeoidea* sp. Tangential section through armor of Yale trunk No. 656, illustrated in two transverse trunk sections on Plate 5, photographs 5, 6. ×0.6.

Trunk 656 recalls the basal segment of a heavy woody cylinder, Yale trunk 154, shown on Plate XIV, Volume I, with which there is further agreement in the very thin cortex; and, for cycads of robust type, it must be admitted that these are both quite unusual specimens because of their extreme wood development. In the case of trunk 154 it was at first thought that reference to *C. ingens* appeared the more reasonable. Now it is found

that *C. ingens* had a fairly heavy basal woody cylinder development, while it seems that *C. Jenneyana* had a rather thin cylinder. It is therefore not quite certain whether the trunk 154 is really a *C. ingens* or some undetermined form of tall habitus and very woody stem. However this may be, specimen No. 656, as illustrated in photograph 5, Plate 5, affords the only example thus far observed of a large Cycadeoid with basal reduction of the medulla to no more than the size seen in conifers. Furthermore, there is an appearance resembling extensive development of growth rings which were present, although of more feeble development than the specimen itself at first suggests. Certainly Cycadeoid types like the foregoing most effectively serve to bridge the gap between stems with a large pith and those with a small pith like that of conifers and dicotyls. Such specimens, moreover, render it nearly certain that on the basis of wood, zone development, and structure it will sooner or later be possible to divide the Cycadeoideas generically. Meanwhile the facts outlined in the introductory chapters apply here. It must not be forgotten that generic and specific names can not be freely applied to these Cycadeoid trunks lacking fruits or divested of their cortices without displacing the older nomenclature by a new one fully as inadequate. The rules and usages in vogue for the study of coniferous woods of the Mesozoic, where the chance of learning the pertaining type of fructification is negligible, can not be applied here with safety. The marvelously conserved structures of the named types must be completely elaborated before applying new names to structural variations observed in incomplete specimens. The inconsistency which would be involved in here giving to the wood zone, Yale trunk 154 (Vol. I, Pl. XIV), a new generic name and to Yale trunk No. 656 still another new generic name, while related stems remain unsectioned, should be patent to every student. And these considerations apply even more stringently to the European series, to which too many incompletely-defined generic names are already given.

It will give further point to the meaning of cycad species based on *outer characters* if at the risk of repetition it be once more emphasized that in the long and varied series of trunks assigned to *C. Jenneyana* and *C. ingens*, one finds a variety of leaf-base characters which renders it virtually impossible to set usable specific limits. In fact there is no discernible dividing line between these "species." If one knew solely of the type trunks of *C. Jenneyana* and *C. excelsa* he could not hesitate in separating from them the great type of *C. ingens* as an unqualifiedly distinct form because of its enormous leaf bases and elliptical and robust, instead of symmetrically columnar form. But with several hundred more or less fragmentary trunks and armor fragments referable to one or the other of these species or varieties before one, the case is different. On the one hand, one notes additional examples identically like the type of *C. Jenneyana*, notably trunk No. 551 of the Yale collection (*Cf.* Plate 4); on the other, such trunks as that shown on Plate 4 are absolutely identical in form, preservation, and appearance with *C. ingens* type. Then, between these two kinds of trunks, are the far greater number of Black Hawk fragments or imperfect trunks, which are strictly intermediate to both, or even present the more obvious characteristics of both on the same trunk. Such an example is Yale specimen No. 110 (Plate 4), which has very large rhombic leaf bases below, *where the armor is partly eroded*, and the smaller, more irregularly shaped leaf bases so characteristic of *C. Jenneyana* type above, where armor conservation is more complete. The trunk is, however, markedly columnar and can for that reason solely be tentatively assigned to *C. Jenneyana*. But it must be noted that if the trunk were broken off a little lower it would have been called *C. ingens* and that if the summit of *C. ingens* type were found isolated and in a slightly different state of erosion it would, so far as its armor characters go, be named *C. Jenneyana*. Furthermore, all this suggests

that the tall trunks of *C. Jenneyana*, when about two-thirds grown, may have had a more elliptical form, and that with subsequent elongation there was sufficient armor excision to finally produce a columnar form. It might be supposed, too, that along with such a change the wood zone of the elliptical *C. ingens* trunk type was late in life slowly added to in such a way as to produce the heavy cylinder like that shown in Volume I, Plate XIV. If so, *C. ingens* might ultimately become a synonym of *C. Jenneyana;* for it does not seem that the smaller number of 10 or 11 microsporophylls seen in some flowers of the tall trunks, until found constant in a large number of flowers, can be relied upon as a specific difference from *C. ingens* with 13 microsporophylls. Part of the uncertainty is no doubt due to the presence amongst the trunks conveniently called either *C. ingens* or *C. Jenneyana*, of variant or distinct forms like Yale trunk 642, mentioned above.

Cycadeoidea formosa Ward.

1898. WARD. Proc. U. S. Nat. Mus., Vol. XXI (No. 1141), pp. 222, 223.
1899. WARD. Ann. Rep. U. S. Geol. Surv., XIX, pp. 634, 635, Pls. CXLIV–CXLVII.
1906. WIELAND. American Fossil Cycads, Vol. I, Pl. VI, photograph 5, and Pl. XIV, photograph 2.

Exteriorly viewed, there is not among all the American collections a more beautiful or characteristic cycadeoidean trunk than No. 89 of the Yale collection; nor has a second specimen quite like it been brought to light. Unfortunately, however, silicification has gone on to the point of chalcedonization, so that although cut and fractured surfaces are far darker than the light weathered surface of flinty texture, the thin sections are rather disappointing. Such as have been cut indicate the leaf-base-bundle pattern to be of the more or less Encephalartean type. Also, the thin cortex and wood zone inclosing the large medulla is well outlined, as shown in Volume I, Plate IV, photograph 2. While these features stand out clearly, little further of structural detail can be gleaned. Many fruits are present, mostly small and young; but the young forms, which must have had cones no more than a centimeter or even less in diameter, show little more than the outer husk of bracts, while several larger fruits have wholly passed over into purely secondary sphærocrystic or more or less rod-like siliceous structures.

Nevertheless, this trunk must be regarded as specifically distinct, its separation from all other Black Hawk forms being indubitable. It is one of the strictly globose stems. The leaf-base differences from other types, particularly *C. cicatricula*, are pronounced. In outer form there is a partial resemblance to the leaf bases of *C. Stilwelli*, but the regular bundle pattern of this latter species proves it different. Nor can the type specimen be a juvenile *C. ingens*, the younger forms of which have a far heavier wood zone and enormous leaf bases. Finally, *C. Jenneyana*, the only remaining form to which reference could be made, is so different that did not the columnar *C. Stilwelli* and *C. ingens* intervene, even generic separation might be considered necessary; for the thin woody cylinder and pauciform ramentum stand in rather striking contrast to the heavy wood of *C. ingens* on the one hand and the profuse ramentum of *C. Jenneyana* on the other.

Comparison with the cycads of other localities of course becomes more complex and unsatisfactory. Professor Ward justly drew attention to the armor type seen in the Minnekahta trunks he called *Cycadeoidea McBridei*, as showing the nearest general resemblance; but these have a quite different leaf-base-bundle pattern, and probably differ markedly in fructification. Among foreign specimens it would seem that no other form than just the original type of *Bennettites Gibsonianus* presents closer agreement in form and size. But while general features are thus strikingly similar in the Isle of Wight cycad, even to the proportion of ramentum, the bundle pattern differs in being regular, like that characteristic

of all Minnekahta specimens thus far studied. It must therefore be concluded that *Cycadeoidea formosa* is a well-marked and valid species, despite the fact that it seemingly appears but once in all the extensive collections from the localities girdling the Black Hills.

Cycadeoidea Stilwelli Ward.

(Plate 5, photographs 1, 2.)

1898. WARD. Proc. U. S. Nat. Mus., Vol. XXI (No. 1141), pp. 223–225.
1899. WARD. Ann. Rep. U. S. Geol. Surv., XIX, pp. 635–637, Pls. CXLVII–CLII.
1906. WIELAND. American Fossil Cycads, Vol. I, Pl. VI, photograph 4, and text-figure 33; 2 showing leaf-base-bundle pattern.

Of the various Yale specimens which were referred by Professor Ward to the present species and illustrated by eleven plates, several, especially the one figured on Plate 5, photographs 1, 2, are distinct. Although an arbitrarily selected trunk series, the specimens called *C. Stilwelli* assuredly include a few very characteristic forms denoting a well-marked, medium-sized columnar trunk type not readily confused with any other. The only likely contestant for any possible priority would be, moreover, some one of those trunks from the Iron Ore Beds of Maryland. But even casual inspection of the Maryland trunks with notably regular leaf-base spirals at once separates these latter because of their heavy ramentum and more triangular leaf-base scars. Of the few with more nearly rhombic outlines none has nearly so pauciform ramentum as *C. Stilwelli*, in which there is in fact nearly complete elimination, with a regularity of leaf-base pattern quite as striking as that of the modern *Macrozamia*.

From its immediate neighbors *C. Stilwelli* is readily separated. It does stand next to *C. cicatricula*, but this form is, relatively speaking, microphyllous; whereas the next nearest form, *C. formosa*, is by comparison megaphyllous, and differs further in having the leaf-base bundles less regularly aligned. The great species *C. ingens* and *C. Jenneyana* differ more widely, particularly in forming a reinforced woody cylinder, and may in part even prove to be separated generically. So far nothing is known of either the leaves or fruits of *C. Stilwelli*, which simply remains as a very handsome trunk type with a narrow cortex, thin woody cylinder, and large pith and medulla.

Cycadeoidea (rhombica) cicatricula (Ward). (Emend. Wieland.)

1898. WARD. Original description in Proc. U. S. Nat. Mus., Vol. XXI, No. 1141, p. 203.
1899. WARD. Ann. Report, U. S. Geol. Surv., XIX, pp. 609, 610, Pls. LXXXIII, LXXXIV.
1901. WARD. *Cycadeoidea rhombica.* Am. Jour. Sci., 4th ser., Vol. X, pp. 336, 337, Pl. 11.
1906. WIELAND. American Fossil Cycads, Vol. I, refigures cotype *C. rhombica*, Pl. V, photograph 4.

In that important paper by Ward entitled "Descriptions of the Species of *Cycadeoidea* or Fossil Cycadean trunks thus far determined from the Lower Cretaceous Rim of the Black Hills," to which we have constantly to refer, the sixth species dealt with is the new form at first represented by the single trunk No. 118 of the Yale collection, and named *C. cicatricula*. With this single and unmistakably unique specimen in view, and bearing in mind that the original tissues have in large part been chalcedonized rather than merely silicified, it is well worth while to recall the compact description originally given:

"Trunks small and short, subconical, more or less laterally compressed, smooth and symmetrical, unbranched, light-yellowish brown on the weathered surfaces, fine-grained and flinty within, about 20 cm. high, 18 by 22 cm. in diameter, with a girth of about 60 cm., and weighing 13 or 14 kg.; organs of the armor nearly horizontal; leaf scars arranged in two definite series of spiral rows, those from left to right forming an angle near the base of about 70° with the axis but curving inward in their upward course so that the angle progressively diminishes to about 30° at the summit, those from right to left only slightly curving and making an angle of about 45°; scars very small, almost

exactly rhombic, uniform and definite with all the angles sharp, distance between lateral angles 9 to 12 mm. and between vertical ones 6 to 8 mm.; leaf bases present filling the scars to near the top, presenting a roughened spongy tissue; ramentaceous walls very thin, varying from the thickness of tin foil to 2 mm., presenting a beautiful and regular network of whitened lines over the entire outer surface of the trunk, with a faint commissure or elongated openings between the contiguous plates of the thicker ones; reproductive organs not abundant nor well developed, the most typical 3 cm. in diameter, variable in shape and character, consisting of protuberances with a depression at the top or ridges with bract scars on the sides, others anomalous, consisting of small projections or elevations, probably abortive, none of them greatly disturbing the form or arrangement of the leaf scars; armor 3 cm. thick, separated from the wood by a definite line or crack; cortical parenchyma 2 cm.; secondary wood 3 cm., consisting of an outer ring 2 cm. thick and an inner one 1 cm., with a fissure between; medulla elliptical, 5 by 7 cm. in diameter, consisting of a homogeneous substance resembling fine yellow sandstone, clearly marked off from the inner ring of wood."

When the above description was given, be it further noted, the nearest related American species known was certainly, as Professor Ward did not fail to observe, the trunk described on a subsequent page as *C. Stilwelli*. But later, when handling a new series of trunks from the Black Hawk region, which greatly extends our knowledge of the macroscopic characters and general appearance of *C. cicatricula*, a palpable error was made in again drawing comparison with *C. Stilwelli*, and proposing a further new species *C. rhombica*. For, distinct and unmistakable as *C. Stilwelli* is, there is among all known American cycadeoidean trunks no more homogeneous series belonging to a single and indisputable species than that to which the names *C. cicatricula* and *C. rhombica* have been given, and for which the former only is valid and required.

With this series before one, namely, Nos. 118, and 629, 620, 623, 627, 630, 631, 640, etc., of the Yale collection, the original description of *C. cicatricula* need only be extended in minor detail, due to the level at which measurements are made, to differing age, and preservation. Plate 5 (photographs 3, 4) shows the characteristic armor and the wood zone.

It is evident that the leaf bases are of remarkably uniform size in the various specimens, that the fruits are few, mostly small (young), and poorly conserved, and especially that these trunks were of columnar habit, with a relatively thin woody zone and a large medulla. They are not certainly known to occur in any other American locality, and their nearest foreign replica seems to be the Russian specimen *Cycadeoidea (Tubicaulis) rhomboidalis*, which is much too remote in both latitude and time to permit any further comparison. While the axillary fruiting branches of *C. cicatricula* are always poorly conserved, there is not the least reason to doubt that they were of the true *Cycadeoidea* form. But they may have been of the long-peduncled type, and the more abundant in the apical region of the trunk.

FIG. 14*a*.—Slope of Lakota sandstones near Minnekahta, South Dakota, looking southeast. Fossil tree in foreground.

The high mesa in the left background is Parker's Peak, an escarpment of Dakota sandstone. There is here an extensive exposure of the "Rim" formations. The Minnekahta Cycad locality centers in the middle Lakota foreground, to the right of the thick patch of pines somewhat in line with Parker's Peak and the fossil tree. Between these pines and the deeper ravine to the right the greatest collections were made. (Compare with Figures 1*a* and 8*a*.) Photographed by N. H. Darton.

CHAPTER VI.

THE MINNEKAHTA CYCADEOIDEAS.

It is a singular and but partially explained fact that the American fossil cycad localities, as well as those of Europe, should be so restricted stratigraphically, while (as commented upon in Volume I) not a single silicified trunk has been reported from Africa, South America, or Australia, and a few Indian specimens represent the sole Asiatic forms. It may be that the robust *Cycadeoidea* type, though certainly as cosmopolitan as the existing cycads, occurred rather sparsely in the upper Jurassic and lower Cretaceous floras, although spreading over the whole world rapidly like the Pleistocene elephants and mastodons, only to suffer quick extinction. But why trunks of the closely related groups, many of which reached large size, as we know from the imprints of trunks in the Mexican Lias, should be so rarely found in the form of imprints or casts, and why no petrified forms of such should be found at all, is most difficult to account for. For all through the Jura occur the stems of many species of conifers, sometimes isolated, but often in striking abundance; while in the Cretaceous such stems may be expected in any fresh-water horizon. In the Triassic the same is true, and the petrified forests of that age, as seen at various points in the southwestern United States, are among the most remarkable known. Especially in the Shinarump formation H. E. Gregory has observed coniferous logs distributed over wide areas in such vast and constant numbers as to form an unfailing horizon marker.

It is not so difficult, however, to understand why the localities which yield silicified cycads in some number are usually restricted in area. In the first place, the conditions requisite to silicification must nearly always have been local rather than general; and secondly, anyone who studies afield must be much struck by the fact that when even such durable fossils as the silicified stems of conifers and cycads weather out of the strata in which they are embedded, they soon break up or are completely disintegrated and lost to view. From the conditions at both the Black Hawk and Minnekahta cycad localities, it is quite clear that literally thousands of specimens must have been eroded out in rather recent time. But of all these only a small number is left behind on the hillsides, a few yards or occasionally a few rods removed from the positions in which the individual specimens were originally embedded. The trunks in the course of years only occasionally roll down the hillsides a distance of a few hundred feet without breaking up. Very rarely a much-weathered fragment may be found at some more considerable distance as a water worn and smoothed boulder. Although I have carefully examined all the gulches, ravines, or dry channels leading out from the several Black Hills localities, even extending the search for long distances from the points where the cycads were seen to weather out, not a single specimen rewarded this search. It is, however, a fact that occasionally the specimens weather out in more or less protected positions, gradually reaching lower levels as the containing strata recede, so that in the course of erosion lasting through tens of thousands of years such specimens are found at considerable distances from any outcrop of the stratum to which they belong. But only the denser specimens can long resist the elements.

In America, as already recounted in some detail, the three great cycad-yielding regions are the Iron Ore Beds of Maryland, the Black Hills Rim, and the Freeze Out Hills of Carbon

County, Wyoming. The lesser localities, yielding single specimens only, number no more than a half dozen in all. The Black Hills Rim, however, includes a whole group of larger and lesser localities, easily the most remarkable known, forming a complete cycad girdle of the hills, along which new and striking discoveries of trunks, either singly or in groups, may be expected at any time. A notable instance is Dr. Darton's recent "find," the remarkable Hermosa cycad of Plate 43. Known for a much shorter time than either the Maryland or Isle of Portland localities, the "rim" has already yielded far more and far handsomer trunks than all the rest of the world beside, by far the greater number of specimens coming from the Minnekahta neighborhood on the south side of the Hills. Here the trunks are not only more numerous than elsewhere, but often exhibit the finest types of conservation, while some of the specimens reach the maximum of size. Here, too, occur the only known branched forms, represented by the magnificent types *Cycadeoidea dacotensis* and *C. Marshiana*, and by several related lesser species. The Minnekahta locality is thus seen to be easily the most striking in the whole world, both as to number of trunks, variety of form, interest of conserved floral types, and the number of species represented. Its study, owing to the striking physiography of the entire region, must at all times prove instructive and interesting, while the collections already made must also long hold the attention of botanists.

It is far too early to give the alignment of the Minnekahta species as closely as has been done in the case of the much simpler columnar series from Black Hawk; but very considerable progress has been made in this direction, and it is possible to give those facts of primary interest which may make the great series of Minnekahta trunks a far less difficult one than it has doubtless seemed to students. Accordingly we may proceed to comment at some length upon the more important specimens, noting finally those less conspicuous trunks of more or less doubtful specific reference.

Cycadeoidea dacotensis (Macbride) Ward.

1893. *Bennettites dacotensis*, Macbride. Am. Geol., Vol. XII, p. 249, Pl. XI, Fig. 1 (non Fig. 2); Bull. Lab. Nat. Hist. State Univ. of Iowa, Vol. II, No. 4, Iowa City, 1893, p. 391, Pl. XII, Fig. 1 (non Fig. 2).
1894. *Cycadeoidea dacotensis* (Macbride) Ward. Proc. Biol. Soc. Washington, Vol. IX, p. 86.
1899. *Cycadeoidea* sp., Wieland. Am. Jour. Sci., Vol. VII, May, p. 389, Figs. 9–16, Pl. X, Figs. 17, 18.
1899. *Cycadeoidea dacotensis* (Macbride) Ward. Ann. Rep. U. S. Geol. Surv., XIX, pp. 602–605, Pls. LXII–LXVI.
1901. *Cycadeoidea dacotensis*, Wieland. Am. Jour. Sci., Vol. XI, June, pp. 428–432, Figs. 1–3.
1900. *Cycadeoidea dacotensis*, Wieland. Yale Sci. Mon., Vol. VI, March, page 7, Fig. 8.
1900. *Cycadeoidea dacotensis*, Ward. Am. Jour. Sci., Vol. X, p. 332 (enumerates specimens in the first 720 numbers of the Yale collection assigned to this species).
1906. *Cycadeoidea dacotensis*, Wieland. American Fossil Cycads, Volume I, pp. 133–134, 144–162, 176–183, 184, and Figs. 14, 28, 30, 34, 70–75, 80–82, 83–89, 94–100, with Pl. V, Fig. 2; Pl. VI, Fig. 8; Pl. XX, Figs. 1–4; Pls. XXXIV–XLII.
1908. *Cycadeoidea dacotensis*, Wieland. Am. Jour. Sci., Vol. XXV, p. 94.
1909. *Cycadeoidea Marshiana*, Capellini. Mem. R. Accad. Sc., Ist. di Bologna, Serie VI, Tomo VI, pp. 15–16, Pl. I, Figs. 1–2.
1909. *Cycadeoidea dacotensis*, Wieland. Am. Jour. Sci., Vol. XXXIII, pp. 74, 75.
1914. *Cycadeoidea dacotensis*, Wieland. Am. Jour. Sci., Vol. XXXVIII, Aug., pp. 121, 122.

Just as any comparative or taxonomic study of Maryland Cycadeoideas must begin with *Cycadeoidea marylandica*, so the investigation of the great group of cycads assembled from the Black Hills Rim must be based on the *Cycadeoidea dacotensis* of Macbride. It is now just an even score of years since Professor Macbride first brought to scientific notice the remarkably interesting Minnekahta cycad locality, beyond question the greatest and most important in the world yielding silicified cycadeous plants. The collections which were then made from the hillsides at Minnekahta, literally strewn with silicified trunks by the hundred, were the pick of that marvelous petrified forest, and included some thirty speci-

mens subsequently turned over to the museum of the State University of Iowa, with the exception of four handsome trunks which were presented to William Carruthers and deposited by him in the British Museum at South Kensington. (See Plate 13.)

Beyond doubt Professor Macbride was in the main correct in describing this collection of trunks under the single specific head *Bennettites dacotensis*, accepting the usage of the British and most continental paleobotanists at the time. In truth, after long study of the silicified cycads, one must freely testify that no other course was fully open. Only after study of larger polished and thin sections does it become possible to determine species from these trunks of darker texture; and indeed the State University of Iowa collection, as made up of the largest and finest specimens, appears to include but two or three of the full dozen species which time and study will eventually show to be included in the Minnekahta group. In going over the Iowa specimens with Professor Macbride several years ago, it appeared possible that in case there is a bona fide species *Cycadeoidea superba*, it may be present; also *C. Wielandi* or *C. Colei* is present. The specimens, however, mainly illustrate in great wealth of form and detail *C. dacotensis*, the most striking of all known Cycadeoideas, because of the number and perfection of the huge branching specimens included, as well as the size and conservation of floral features; but the exact specific characters of *Cycadeoidea dacotensis* can never be so quickly and profitably determined as from the type itself. This it may justly be held should be cut through longitudinally with care, after a *papier mâché* model has been made—a most feasible proceeding, as Capellini of Bologna and his preparateurs have developed the finest skill in the reproduction in *papier mâché* of the exact features and nearly the coloring of the Italian silicified trunks in the Capellini Museum at Bologna. This entire series has been reproduced, and on the occasion of a visit to Bologna a set of these replicas was secured for addition to the demonstration material in the Yale Museum. Such replicas being once made, the original types become available for sawing and cutting of an indefinite number of sections from the least striking half of the trunk, the best half being retained for exhibition and record. Not only so, but the location of all fruits or leaves studied can be recorded and all records kept complete.

It is therefore clear that a specimen of such rare interest as the type of *C. dacotensis*, if not lost by some untoward event, will some day be cut, even though it be a hundred years hence. And it is equally clear that the longer such study is deferred the less valuable will the original type become and the greater will be the difficulty in keeping the synonymy of *C. dacotensis* simplified.

The question of cycad exhibition in museums *versus* cycad investigation has already been considered in the prefatory chapters and need not be reconsidered now. The great type *Cycadeoidea Reichenbachiana* is an example in question. With 160 years of museum history this famous fossil cycad is still unstudied. Who can measure the impetus that would have been given, not only to paleobotany but to the entire subject of paleontology, had the attention of a Witham been directed to the study of the great type of the Zwinger Museum! It is now 83 years since Witham made his first thin sections, his methods being for a long time more followed by petrographers than botanists, and it is probable that even in the days of Witham adequate study of so large a trunk as *Cycadeoidea Reichenbachiana* could have been carried out. It will be recalled that all the earlier studies of the structure of American fossil cycads were accomplished with some success by the aid of methods as simple as those Witham employed.

However, to-day it is fair to say that there is no limit that need be set to the size of thin sections and the accuracy with which they can be prepared; while even etching of

polished surfaces or staining or coloring methods, such as are applied to agate, may be employed. It is, therefore, a work of supererogation to attempt to identify cotypes of *Cycadeoidea dacotensis* in varying stages of fructification. Presumably the macroscopic characters of the original type, as shown in the photograph by Professor Kay (Fig. 1), are in the main sufficiently clear for identifying other specimens of this species within the limits of accuracy demanded by museum cataloguers; but it would be more satisfactory to know from type sections the true size of the medulla, the development of the woody cylinder, the wood structure, presence or absence of wood parenchyma, the features of tracheidal pitting with variations from base to apex of the trunk, the features of the cortical parenchyma, especially as displayed by the oblique transverse section cutting the leaf base and peduncle supplies at various heights, the transverse leaf-base sections with the bundle patterns, sections of peduncles, and finally the structure of those bract-enveloped but huge and magnificent fossil flowers which make *C. dacotensis* type next to *C. ingens*, and *C. Dartoni* one of the most remarkable of fossil plants of any kind ever recovered.

FIG. 15.—*Cycadeoidea dacotensis*. Yale Museum Trunk No. 158. ×⅔.
Tracing from obliquely cut longitudinal section of trunk. The section quite exactly passes through the summit and at the base cuts the inner cortex. Medulla, xylem, phloem, cortex, and armor so marked; cambium shown as dotted line.

In the face of this formidable array of unknown detail, to pronounce this or that specimen as a *C. dacotensis* must be a somewhat doubtful proceeding, even after the types closely associated with and most nearly resembling *C. dacotensis* have received their meed of study. The closer study of the type of *C. dacotensis* will thus in time hold much less of importance than now, in case it is delayed, but will still be a desideratum to the fuller knowledge of fossil cycads. So at least stands the case for *Cycadeoidea Reichenbachiana*. Meanwhile the residuum of doubt which pertains to the identification of the

larger branching trunks of the Minnekahta series may be discussed further in annotating the species named *Cycadeoidea Marshiana* and *C. colossalis*.

Text-figure 15 doubtless shows the longitudinal section of a very handsome *Cycadeoidea dacotensis* trunk with its disks just shed. Only the features plainly visible on the polished surface are shown. The axes of 10 young fruits or small branches with large bract systems are cut, but in only one (*O. S.*) is there a plainly visible young ovulate cone, with its seed zone 1 mm. in thickness. This is plainly one of the most highly specialized of all the Cycadeoids, the medulla and cortex being heavy and the wood zone thin, while the armor makes up a full half of the diameter. The woody cylinders of the large peduncles or branches in at least three clear instances on the left side of the figure originate directly on the main woody cylinder, though coming closely in contact with the axillary leaf trace.

The trunk which yielded this section was sent to Professor Capellini at Bologna, where it was sawed in two and the two faces polished, the one half being placed on exhibition in the Capellini Museum and the other half being returned to the Yale Museum. As will be seen from the drawing, the polished surface is slightly oblique, although not enough so to really obscure any of the features or proportions of the medulla and woody cylinder. Capellini gives a fine photograph of the trunk before cutting and a figure of the polished surface of the half in the Capellini Museum under the name *Cycadeoidea Marshiana* as cited in the synonymy, the identification being mine. But I regret to say that, as explained further on in the annotations on *Cycadeoidea Marshiana*, my earlier attribution must be changed. [The fructifications of the primary type of *Cycadeoidea Marshiana* were supposed for a time to agree with those of various trunks which, to be consistent in the use of macroscopic characters, should be referred to *C. dacotensis*.]

Professor Ward (*Cf.* synonymy, *supra*) called this specimen a *C. minnekahtensis*, but, as seen in the appended list of matched trunks, which I made after his determinations had been completed, he was by no means certain in the application of his own diagnoses of species. As now subjoined, the list explains itself, and should be regarded as one of the incidents in the study of fossils which other paleontologists need to take to heart just as much as the paleobotanist. It would have been a much more serious error to contentedly assume that the magnificent totality of nearly an even thousand specimens yielded from first to last by the Minnekahta forest was without marked specific variety. The reductions in the Yale numerical list, after a month spent in careful matching of the fragments in all of the collections made during the several years of active cycad collection, follow:

1. *C. colossalis* (trunk No. 9) + *C. Marshiana* (trunk No. 33) = *Cycadeoidea Marshiana* No. 33.
2. *C. dacotensis* (trunk No. 13) + *C. colossalis* (trunk No. 17) + *C. colossalis* (trunk No. 40) = *Cycadeoidea colossalis* No. 40.
3. *C. Marshiana* (trunk No. 47) + *C. minnekahtensis* (trunk No. 142) = *Cycadeoidea colossalis* No. 142.
4. *C. minnekahtensis* (trunks Nos. 71, 72) + *C. Marshiana* (*?*) (trunk No. 217) = *Cycadeoidea minnekahtensis* No. 217.
5. *C. minnekahtensis* (trunk No. 140) + *C. Marshiana* (*?*) (trunk No. 404) = *Cycadeoidea minnekahtensis* No. 140.
6. *C. minnekahtensis* (trunk No. 143) + *C. Marshiana* (trunk No. 164) + *C. McBridei* (No. 267) + *C. minnekahtensis* (trunk No. 281) + *C. minnekahtensis* (trunk No. 285) + *C. Marshiana* (trunk No. 392) + *C. minnekahtensis* (*?*) (trunk No. 411) + *C. Macbridei* (trunk No. 224) + *C. Colei* (trunk No. 240) + *C. Colei* (trunk No. 256) + indeterminable specimen No. 410 = *Cycadeoidea Marshiana* No. 164.
7. *C. superba* (trunk No. 137) + *C. superba* (trunk No. 146) = *Cycadeoidea superba* No. 137.
8. *C. minnekahtensis* (trunk No. 181) + indeterminable specimen No. 440 + *C. minnekahtensis* (trunk No. 230) + *C. McBridei* (trunk No. 491) = *Cycadeoidea minnekahtensis* No. 181.
9. *C. minnekahtensis* (trunk No. 220) + *C. superba* (trunk No. 264) = *Cycadeoidea minnekahtensis* No. 220.
10. *C. Paynei* (trunk No. 239) + indeterminable specimen No. 418 + *C. Paynei* (*?*) (trunk No. 461) + *C. colossalis* (*??*) (trunk No. 236) + *C. Marshiana* (*?*) + *C. excelsa* (trunk No. 453) + indeterminable specimen No. 455 + *C. excelsa* (trunk No. 481) + indeterminable specimen No. 479 and No. 498 = *Cycadeoidea excelsa* No. 481.
11. *C. minnekahtensis* (trunk No. 324) + *C. dacotensis* (trunk No. 356) = *Cycadeoidea dacotensis* No. 356.

12. *C. minnekahtensis* (trunk No. 332) + *C. minnekahtensis* (trunk No. 349) = *Cycadeoidea minnekahtensis* No. 332.
13. *C. turrita* (trunk No. 70) + *C. minnekahtensis* (trunk No. 480) = *Cycadeoidea minnekahtensis* No. 480.
14. *C. minnekahtensis* (trunk No. 397) + *C. dacotensis* (trunk No. 445) = *Cycadeoidea minnekahtensis* No. 397.
15. *C. Colei* (trunk No. 405) + *C. Marshiana* (trunk No. 711, a branch) = *Cycadeoidea Marshiana* No. 711.
16. *C. Jenneyana* (trunk No. 553) + *C. Jenneyana* (trunk No. 658) = *Cycadeoidea Jenneyana* No. 553.
17. *C. Macbridei* (trunk No. 224) + *C. Colei* (trunk No. 240) = *Cycadeoidea Colei* No. 224.
18. *C. McBridei* (trunk No. 232) + *C. minnekahtensis* (trunk No. 355) = *Cycadeoidea dacotensis* No. 232.
19. *C. colossalis* (trunk No. 10) + *C. Macbridei* (trunk No. 238) = *Cycadeoidea colossalis* No. 10.
20. *C. dacotensis* (trunk No. 525) + *C. dacotensis* (trunk No. 528) = *Cycadeoidea dacotensis* No. 502.
21. *C. Marshiana* (trunk No. 502) + *C. minnekahtensis* (?) (trunk No. 507) = *Cycadeoidea Marshiana* No. 502.
22. *C. Colei* (?) (trunk No. 256) + indeterminable specimen No. 410 = *Cycadeoidea Colei* (?) No. 256.
23. *C. Marshiana* (?) (trunk No. 423) + *C. Paynei* (?) (trunk No. 337) = *Cycadeoidea Paynei* No. 337.
24. *C. Wellsii* (trunk No. 548) + *C. dacotensis* (trunk No. 549) + *C. dacotensis* (trunk No. 550) = *Cycadeoidea dacotensis* No. 549.

A study of the foregoing list shows well how difficult may prove the attempt to determine species of silicified cycad trunks, whether from the Black Hills, from the Iron Ore belt of Maryland, or from the Isle of Portland, on the basis of outer features alone.

Cycadeoidea Marshiana (Ward).

1898. WARD. Proc. U. S. Nat. Mus., Vol. XXI, pp. 208–210.
1899. WARD. Ann. Rep. U. S. Geol. Surv., XIX, pp. 616–618, Pls. CI–CV.
1900. WIELAND. Yale Sci. Mon., Mar., pp. 1–11, Figs. 7, 9, 13.
1900. WARD. Am. Jour. Sci., Vol. X, Nov., p. 332 (enumeration of catalogue Nos. of Yale Collection).
1906. WIELAND. American Fossil Cycads, Vol. I, Carnegie Inst. Wash. Pub. No. 34, pp. 135, 136, with Figs. 67, 67*a* (probably *C. dacotensis*); Pl. V, photograph 1 (but not Pl. V, photograph 3, which is probably *C. colossalis*); Pl. VI, photographs 7, 9; Pls. VII, VIII, IX, photograph 1; Pl. XII (which may prove to be some other form, as *C. superba*), and Pl. XXXIII (which may be *C. dacotensis*).
1912. WIELAND. Am. Jour. Sci., Vol. XXXIII, pp. 75–87, Figs. 1–9.

In annotating the literature of *Cycadeoidea dacotensis*, and further illustrating that most conspicuous of all the American species, it was shown that the numerous references to it of trunks now scattered in different collections rest under a certain degree of doubt, so long as the original type remains unsectioned and therefore virtually unstudied. In actuality the species *Cycadeoidea dacotensis* is that single trunk of the State University of Iowa collection shown in Figure 1, and it must be admitted that in stating that any other trunk is conspecific one incurs a certain risk of error. For the case may be as in the far smaller and much better known group of only four or five trunks first referred to *C. Wielandi*, within which two distinct specific forms are found.

Similarly the great aggregate of trunks called *C. Marshiana* includes at least two forms which may be declared specifically distinct by reason of their flowers. One of these is the fine branching trunk No. 11 of the Yale collection, signalized as "the type" of *Cycadeoidea Marshiana*. This has flowers of medium size at first thought to have the same structure as those with disks of 18 staminate fronds and large size cut from Yale trunk No. 214, illustrated at length on Plates XXXV–XLII, Volume I. Closer examination, however, shows that the microsporophylls are broad and few in number, not more than ten. The exact number is not fully evident from the sections at hand; but this type is now recognized as urgently demanding further study. The other specific type appears distinct from trunk 11 because of its smaller flowers with disks composed of 10 or 11 microsporophylls. Nor can we readily determine similarity to either *C. colossalis* or *C. Wellsii*, the only other trunks of large size which have middle- or small-sized disks, except possibly *C. minnekahtensis*, which is yet another species that, like *C. dacotensis*, goes back to a single unstudied specimen. It is much too early to effect a rigid separation.

These general facts first came to light several years ago while making a more thorough study of the smaller fruits previously supposed to be young, but then found to represent

several distinct species of nearly full-grown flowers. In fact, even at this late day, I can do no better than to repeat the general statement then made:

"Bearing in mind that the present rectification is only one of convenience, this same fate of relegation to *Cycadeoidea dacotensis* apparently awaits the fine National Museum trunk nominated as "the type and only perfect specimen" of *Cycadeoidea minnekahtensis;* for it too is a form with medium to large-sized fructifications, and of the two accompanying fragmentary paratypes the fine armor slab numbered 24 in the Yale collections and also figured in the original description has been studied at length and found to be a *C. dacotensis.* Nor can we reconcile either *C. colossalis* or *Wellsii,* the only other species of antecedent description, with the lesser flowered forms to which we wish to turn our attention.

"It thus follows from the material now before us and the trunks secondarily referred to by Ward in his original descriptions, as well as from the chronologic order of type discussion, that while *Cycadeoidea Marshiana* is an unassailably well-founded species, its actual characters are very different from those for several years thought to mark it. Instead of being near to and difficultly distinguishable from *C. dacotensis* with large flowers of eighteen to twenty microsporophylls, *C. Marshiana* proves to be a small-flowered type with only eleven or twelve microsporophylls of distinctly reduced form. In fact these flowers are, as described below, the smallest of any in the silicified series so far found complete. That several of the trunks of much smaller growth with far smaller fronds, like *C. rhombica* and the evidently branched *C. nana,* bore even smaller flowers, is known from various small fruits and ovulate cones, but not so far from complete flowers.

FIG. 16.—*Cycadeoidea Marshiana.* Bisporangiate flower-bud characters. A and B are two buds from trunk 164 of the Yale collection illustrated on Plates VII and VIII, Vol. I. The thin section C is from Yale trunk 3.

A. Drawing of part of armor surface of branch C, Plate VII, Vol. I, showing the rather large heaped synangia of a bud with apex eroded away. Per pheral pittings corresponding to the rachides of 11 microsporophylls plainly appear. Natural size.

B. Transverse thin section of flower with 9 microsporophylls. Same trunk as preceding. The section passes at some distance above the ovulate cone and no decurved tips of microsporophylls appear at the center. The flower is young. Enlarged about twice.

C. Section 761, Yale trunk No. 3. This transverse section belongs to the series illustrated in the succeeding figure, where in the longitudinal section the line A 761 is the base line. At the center the decurved tips of the ornately sculptured microsporophylls, 12 in number, appear. Laterally the rachides of two microsporophylls are cut, evidently near the point where the exterior median furrow begins. *Cf.* next lower transverse section 726 of succeeding figure. × 10.

"These latter, however, appear to be distinct, in consequence of which *C. Marshiana* is now based on (1) the trunks mentioned above as figured under that name in my American Fossil Cycads, (2) those illustrated here, (3) certain other Yale specimens enumerated by Ward, and (4) the magnificent quadruply-branched specimen several years since transferred from the Yale collections to those of the Paris Museum; while a further specimen requiring examination in this connection is the U. S. National Museum trunk No. 2 figured by Ward as the type of *C. Colei.*

"Nor does it, adding yet another word, seem even remotely probable that any of the earlier named Maryland or European Cycads agree with or could ever be found to preoccupy *C. Marshiana;* for the Maryland forms appear to be, in agreement with all European forms, distinctly columnar, while *Cycadeoidea marylandica* (Font.) Capellini et Solms is most like *Cycadeoidea etrusca* Capellini

et Solms, the flowers of which have been briefly restudied by the writer, thanks to the interest of Capellini." (*Cf.* Historic Fossil Cycads, in American Journal of Science for February 1908.)

"Thus the larger branching specimens from Minnekahta are mainly included in the huge, large-flowered *Cycadeoidea dacotensis*, which [possibly] includes *C. colossalis*, *C. minnekahtensis*, and several other species, with *C. superba* as a closely related type. The medium-sized specimens, bearing in mind that it is the adult fruit-bearing plant that is spoken of, mostly belong to *Cycadeoidea Marshiana;* and following this well-represented type comes, amongst smaller forms of branching trunks, the interesting *C. nana.*

"Though before turning to the description of the flowers of *Cycadeoidea Marshiana*, which is one of the main objects of this study, it may, however, conduce to clearness both now and hereafter to observe that the changes in specific assignments which must inevitably follow the closer study of the silicified cycads can scarcely be regarded as taking away from the net value of Professor Ward's earlier determinations and descriptions based on macroscopic characters alone. In 1899 the writer published his opinion that it was fortunate for scientific uniformity that Professor Ward had studied the entire American series then known; and this view still seems just. True enough, when the trunks of the greater Yale collections assembled by 1902 came to be searched rigorously for the purpose of matching isolated parts of trunks, the catalogue list was reduced by about forty numbers, it being found that in some instances parts of one and the same trunk had reached the Museum in different collections, sometimes received several years apart. And it also became evident that the great branching trunks of the Minnekahta series as thus frequently dissociated in the course of collecting had in considerable part simply defied accurate assignment on the basis of outer characters.

"But, on the other hand, all subsequent study has indicated the substantial accuracy of the entire specific alignment first proposed for the unbranched series of trunks from Black Hawk, including *Cycadeoidea Jenneyana, ingens, aspera, formosa, Stilwelli, excelsa,* and *rhombica;* so that in the end the somewhat arbitrary use of macroscopic characters has proven an indispensable convenience. For not only is there rather more connectedness in the determination of the American series of species than in the nearly equal number of European forms, but these latter are on last analysis quite as distinctly based on macroscopic diagnoses and even more destined to revision."

Such is a general statement of what is at present understood by the species *Cycadeoidea Marshiana*, although it is next in order to cut the sections illustrating the woody cylinder, known to be thin, and also to find and to study further mature flowers. The younger ovulate cones and the fairly well-grown staminate disks are quite well known from Yale trunk No. 3 (Plate 26), if, as adjudged from macroscopic characters, this is really a *C. Marshiana*. This trunk was referred by Ward to *C. dacotensis* (Elaboration of Fossil Cycads in the Yale Museum, Amer. Jour. Sci., Nov. 1900, p. 332), but can not belong to this species even if the State University of Iowa type should prove to have disks of only 10 or 12 stamens, which is unlikely. Accordingly it seems preferable to transfer the specimen to *C. Marshiana*, with the general form and flowers of which we know well there is agreement within close specific limits, rather than to call so fine a specimen "undeterminable." It has, of course, been the method throughout this work to uniformly avoid the transference of specimens before very conclusive studies have been carried out; but in the present instance any future change of specific reference can be readily made, since the floral series is now fairly elaborated, and so striking that it must always remain one of the great and outstanding units in the development of a full knowledge of fructification in the Cycadeoideæ. The account of the floral features in this trunk and in one of the original type series of *C. Marshiana*, trunk No. 164 of the Yale collection (shown in Plates VII and VIII of Volume I), which now follows, is given, with some lesser additions, in substantially the form published in Part VI of my preliminary studies. (*Cf.* Amer. Jour. of Sci., Vol. XXXIII, Feb. 1912.)

FLORAL FEATURES.

Flowers of Yale Museum Trunk No. 3.

The *Cycadeoidea Marshiana* trunk No. 3 of the Yale collection, as at once appears in Plate 26, bears many partly eroded bract groups irregularly scattered all over the lateral armor surface, plainly indicating the position of the deeply embedded fructifications.

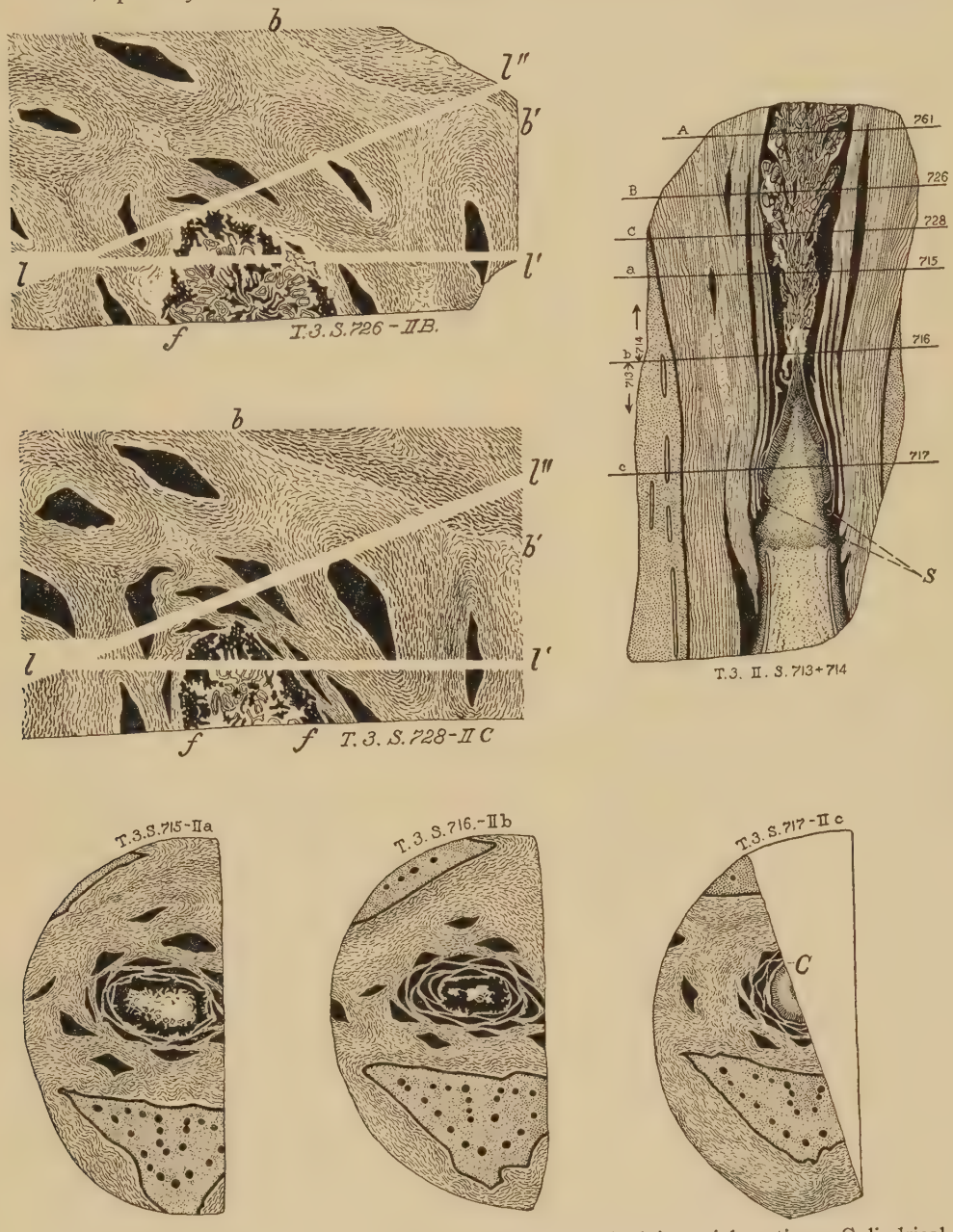


Fig. 17.—*Cycadeoidea Marshiana.* Bisporangiate flower bud in serial section. Cylindrical core No. II, Yale trunk No. 3.

Of the various axes drilled from trunk 3 this is the only one so far found in the bisporangiate condition. For exact position on trunk see Plate 26. Observe that this is a very small bud 5 cm. long. Longitudinal section 713 + 714 and transverse sections 717, 716, and 715 are × ⅔; transverse sections 728 and 726, × 3. See also section 761 of this series given in figure 16. The fruit being small and hidden at the center of the bract mass, several trial sections had to be cut. These account for the lines *l*, *l''*, in sections 726 and 728.

Attention was first directed to these rather inconspicuous flowers while searching for younger fruits of *C. dacotensis*, it being at the time overlooked that such, even when very young, develop a huge pedunclar axis, as in the examples shown in Plate XXXIX, Figure 1, and on Plate XLI, Volume I. A partly unexpected result was therefore obtained when the cutting of sections from core No. II of the series here illustrated revealed the presence of the quite full-sized, though apparently not fully matured, complete flower of Figures 16 and 17. But unluckily the first section, a longitudinal one, did not chance to traverse the floral axis; and it was not until several additional sections were cut that the peripheral synangia were finally observed and the position of the small flowers, no larger than a 5 cm. length of a medium-sized lead pencil, accurately located in the core. Consequently it was hoped that, in the course of the further study of trunk No. 3, a second bud might be found with a non-dehiscent disk in good conservation permitting more perfect sectioning; for the correct technique, of course, requires two transverse sections for the exact location of the first or any other longitudinal section; and the study was carried on until three additional cores were drilled out, these including the lesser cores of Figure 18, and the very large one illustrated in Figure 19, which alone contains four separate strobili. But none of the new cores yielded an additional disk, although no less than nine more axes were found present, making a total of ten fruits studied in the four cores removed from trunk 3. Only in a single instance was even a trace of a disk found persistent; in section 722, cut from the fourth and last core, one sees a considerable mass of broken-down disk tissue just above the cone as indicated at *S*, Figure 18 (S. 722). Evidently the disks at times slowly shriveled up in their much inclosed position instead of being early disengaged after pollinial growth. In the eight other axes seed growth had continued well beyond the disk-dehiscing stage evident in Figure 18 (S. 728); though the basal collar is always distinct, it being held certain that the flowers uniformly bore disks—were truly bi- or "amphisporangiate." In the sections cut from the largest cone, Figure 19 (S. 756), the testal walls are clearly outlined by zonal conservation and one may plainly see the more or less collapsed nucellar sacks in the seed interiors.

Notwithstanding this well-advanced ovulate growth of the great majority of the axes of trunk 3, it still seems probable that among the numerous remaining bract groups, various of which are indicated by the arrows of Plate 26, a few may still inclose complete flowers. But in view of the results recited, further search was abandoned and the parts of core No. II were cemented together again in their natural place for the completion of the oriented sections, showing the structure of the entire flower bud, as now to be described.

The orientation of the series of sections of the sole complete flower obtained from trunk 3 will at once be apparent on inspection of the figures. And it will doubtless be granted that the lesser difficulty of limitation to this single example is more than compensated for by the resultant fixing of the period of disk dehiscence at a given immature stage of ovulate growth, even more accurately than in *Cycadeoidea dacotensis*. Moreover, the series taken as a whole is nearly enough ideal to display the floral features with precision; while the traversal of transverse sections 717, 726, and 728 (Fig. 17) by trial saw-cuts and the necessity of using approximately tandem sections for the longitudinal view has in nowise taken away from Mr. Barkentin's drawings.

The silicification of the armor of trunk No. 3 does not extend to the clear indication of the finer tissues of the inclosed flowers, although all larger tissue zones and features are clearly stained and outlined; so that in the bisporangiate bud one clearly sees the main anatomical details, the peduncle with its wood zones, the course at least of the bundles given off, the bracts enveloped deeply in hairy ramentum, the outlines of the disk and component

fronds with the position of the disk and rachidal bundles (Fig. 16 C, section 761), the pinnules and attached synangia with quite well-marked traces of wall structure, and finally the central ovulate cone with its large pithy axis bearing the young zone of seed stems and interseminal scales; and we can also see traces of the sporangia, either a young condition being indicated, or pollen shedding and sporangial collapse having occurred. The seeds show but little structure, being distinctly younger than those of Figure 19, which show the testal zones and distinct nucellar sacks.

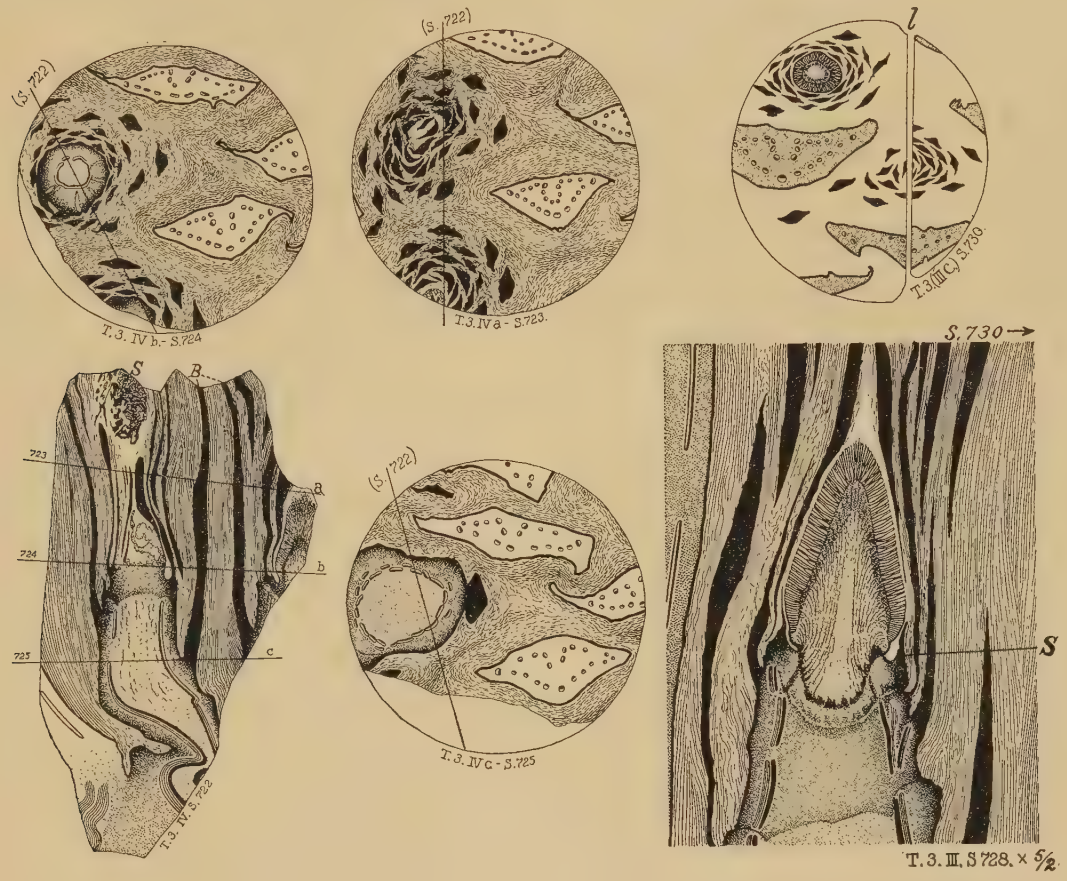


FIG. 18.—*Cycadeoidea Marshiana.* Serial sections of fruit-containing cylindrical cores drilled from Yale trunk 3—continued.

The sections are from two cores, Nos. III and IV, and all are shown about natural size except section 728. Transverse sections 723–725 and the complementary longitudinal section traverse core No. IV. Transverse section 730 and longitudinal section 728 (enlarged) are from core No. III.

The secant lines of the circular sections indicate exactly the position of the longitudinal sections as numbered. The planes of the transverse sections are also indicated and numbered in the longitudinal sections. Each of the cores contains two ovulate strobili, but in section 722 there are disk remnants *S* above the summit of one of the strobili, and perhaps such would also appear in the adjacent ovulate axis were its summit complete. Apparently all four fruits of these two cores were bisporangiate, maturing both disks and cones.

Cell walls are, however, generally obscure; one can not make out the bract structure; and similarly the disk and rachides, though very clearly outlined, appear only as an indistinctly granular groundmass traversed by lighter-colored traces of the bundles, fortunately continuous enough to show the pattern of the bundle system. But even so the assemblage of fairly well-conserved features, taken together with the entire outline of all organs, affords a clear view of the form and general structure of the flower.

On noting that seven rachides are to be seen in sections 726 and 728, and then comparing the series of decurved apices in section 761, Figure 16, it becomes evident that the

disk divides into 12 small microsporophylls, as in the young and quite small flower of *Cycadella wyomingensis* (Vol. I, Fig. 93 I) and the very large-flowered *C. ingens* of the columnar series, instead of dividing into 17 or 18 large staminate fronds as in *C. dacotensis* and various of the *Williamsonia* staminate disks or flowers. The point at which the campanula splits into the separate fronds is accurately located between sections 715 and 728, Figure 16, at a

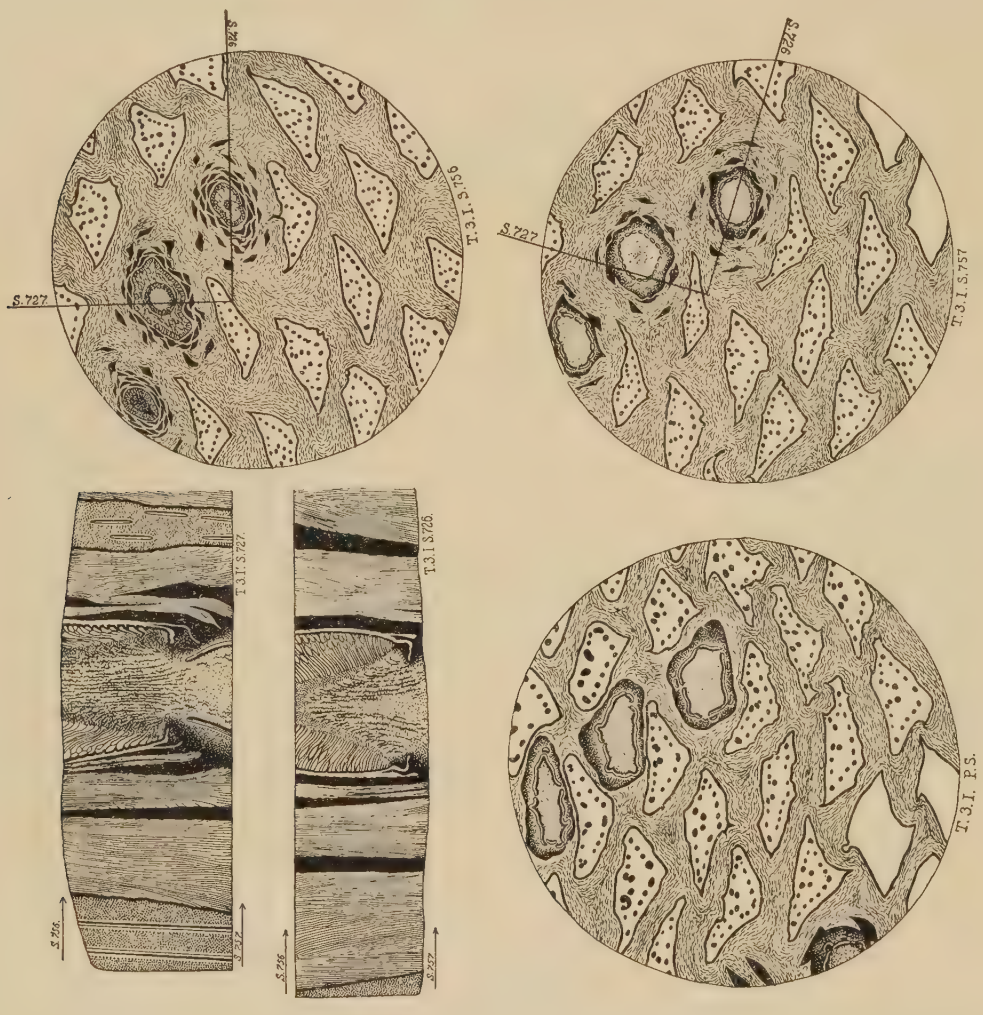


FIG. 19.—*Cycadeoidea Marshiana.* Illustration of serial sections of fruit-containing cylindrical cores drilled from Yale trunk 3—continued.

Transverse and radial longitudinal sections of a large armor core, No. I, 8 cm. in diameter. As figured the transverse sections are reduced to three-fourths natural size, and the two longitudinal sections 726, 727 are enlarged to about twice the natural size. Observe the relation of these armor sections to each other. Section 756 traverses the ovulate zone of three adjacent cones the peduncles of which are cut by the succeeding transverse section 757. The planes of these two sections are about 10 mm. apart; while from the intervening core-segment the two radial longitudinal sections 726, 727 were so oriented at a right angle that each traverses an ovulate cone. Finally the surface of a transverse saw-cut passing about 2 cm. below section 757 was polished (PS). From these complementary drawings alone an exact model of a core-segment about 3 cm. long can be reconstructed, inasmuch as the two sides of the right angle in the transverse sections indicate as numbered the position of the longitudinal sections, and none of the sections can be misplaced if the direction in which the numbers read is retained. As in the five preceding strobili from trunk 3, the disk insertion is distinct.

height of about 1 cm. above the apex of the ovulate cone, which is not a precisely fixable point because ending as a long, thin brush of sterile organs at last almost hair-like.

The length of the microsporophylls can only be estimated within fairly close limits because of the destruction of the mid-region of the bud-summit by erosion; but estimating

this loss at about 1 cm. and adding for the decurved tips 1.5 cm., the full length of the microporosphylls appears to have been about 5.5 cm. Whence, after allowing for the diameter of the ovulate cone, the flower as imagined in an arbitrarily expanded form would have a diameter of 10 or 12 cm.

The rachis and pinnules, as one readily sees in the transverse sections, Figures 16, 17, are much molded and furrowed by appression faces or even crinkled, but withal in a manner producing ornate patterns where these organs are cut to advantage in regular series. The pinnules are broad of base and must tend to confluence with each other. They are 1 cm. long in the mid-rachidal region and diminish much in length towards both base and apex of the frond, so that each frond if laid out flat would have a more or less elongate-elliptical, acuminately tipped, pinnately parted to pinnately divided form, leaving out of account, of course, the closely appressed median spur-like rachidal appendages which doubtless formed a more or less conspicuous feature of the individual fronds and rose to form a dome, as in the flowers ascribed to *C. colossalis*.

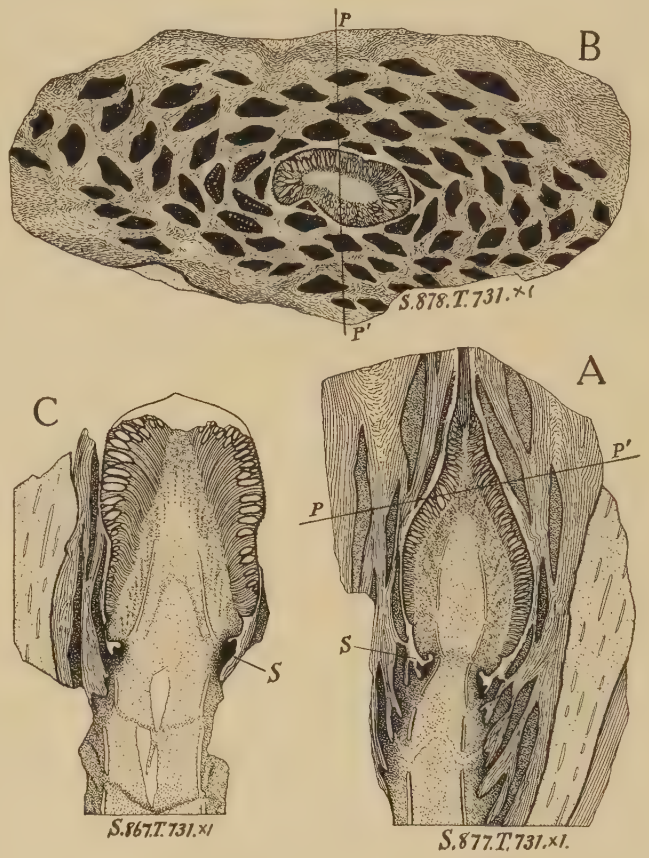


FIG. 20.—*Cycadeoidea turrita* (??). Ward det. Yale trunk 731. Minnekahta. Longitudinal sections of two ovulate cones with the transverse section of one of these. All natural size.

The synangia are well enough advanced in growth to outline themselves distinctly, being in reality better conserved than one might expect from the condition of some of the other tissues. But the individual sporangia can not be clearly made out, and no distinct pollen appears. Inasmuch, therefore, as the synangia have only from half to two-thirds the size seen in *C. dacotensis* buds, in which the size agrees with that of Marattiaceous synangial types, a somewhat young stage of growth may be indicated. One may also surmise an incompletely developed stage due to some failure in floral growth such as would readily have been produced by events leading up to fossilization.

On the other hand, the possibility that the synangia, like the flowers, were of small size, and the pollen all shed, should not be lost sight of; and as bearing on this point the supplementary section No. 717 was cut in order to better bring out the fact that the disk bears the same appearance of wilting and dehiscing just above the insertion, as in *C. dacotensis* buds, where an approach to floral maturity is evident.

But in neither case is it necessary to assume that the staminate frond was normally of much larger size than here seen, while the ovulate zone is already notably older than in the *C. dacotensis* buds, it even being possible that the mature strobilus of trunk 3 did not reach

a markedly greater size than in the largest of the ten axes so far studied. A fairly well-grown or mature *C. dacotensis* cone is shown in Volume I, page 67, under the name *C. Marshiana*, and on the opposite page, 66, under the latter name, a form that belongs to some third species not yet satisfactorily determined.

Cone species and the later growth of cones is, however, a long and difficult subject which can, of course, be much further developed in the course of time. Such axes as those of Figure 20 show well a succeeding stage of growth. In this figure, B is the transverse section through fruit A on the plane PP′, and longitudinal section A is cut on the plane PP′ of B. Only the longitudinal section of fruit C is shown. In A and C basal remnants of campanulate disks appear and it is interesting to note in the original sections that these remnants or wilted insertions (S, S) are more clearly preserved in section A, where seed-stem growth is least advanced, than in section C, where the seed zone has grown forward. But in both cases the disk insertion is clear and in the cone A seed-stem elongation is already begun. The cone C is probably advanced at least several weeks beyond A and it is quite certain that both these axes earlier bore staminate disks. Figure 91, Volume I, shows a still earlier growth stage of precisely this type of cone, where a disk somewhat imperfectly conserved is present. The trunk from which these cones were cut is a medium-sized one weighing 45 kg., doubtfully referable to *C. Marshiana*.

Flower-Buds of Yale Museum Trunk No. 164.

This superb silicified cycad was made the subject of special description with reference to branching in Volume I, pages 41–43, and illustrated in relief on Plates VII and VIII. Here, too, small fruits were supposed to be young until several thin sections showed the presence of mature flowers adjudged to be of the same species as those of trunk No. 3. Although sections of the ovulate cones yet require to be cut, this task is not relatively urgent, since no change of name is involved in the specific reference of this cycad here and earlier made.

The only section cut is that of Figure 16 B, showing distinct agreement of the staminate disk with the corresponding transverse section from the flower of trunk 3 seen in Figure 17, section 728. And the meaning of the section was further confirmed by a rigid search all over the surface of the trunk, taken point by point, resulting in the detection of a single additional example, clear of outline but previously overlooked. This flower has not been cut from the trunk, where it appears just as shown in Figure 16 A. The synangia are apparently larger than in trunk 3, which is really yet another reason for supposing the flower of that trunk to be not quite fully grown. But caution in judging without thin sections is required, here or in the case of any flower or strobilus—more especially where but a few axes are studied. The number of disk divisions is clearly eleven; so that while the study of this form still rests mainly on macroscopic features, there is little doubt as to its identity.

Figure 21 shows the probable appearance of the full-grown bisporangiate bud. Only the paired spurs of the 10 to 12 disk members rise to form the dome. This restoration is about the natural size for a flower with ovulate cone like that of the preceding figure and should be compared with Figure 70, Volume I. The latter figure must doubtless be amended, but it is hardly probable that in the case of the larger flower buds the *ceratoid* spurs were relatively as conspicuous as in medium-sized or smaller flower buds. Nor is it known that the disks were characteristically ceratophyllous in the Williamsonias, although the presence of a dome is suspected in the case of *Williamsonia gigas*. (402, Pl. 53, Figs. 6–8.)

With these fairly detailed descriptions of more or less fully grown amphisporangiate flowers, the consideration of *Cycadeoidea Marshiana* may for the present be closed; though it is of interest to recall the somewhat younger flower of the type specimen *Cycadella wyomingensis* figured on page 175, Volume I. That flower is comparable in size, but has a much more regular outer disk surface and a few more microsporophylls. A second example has not been found.

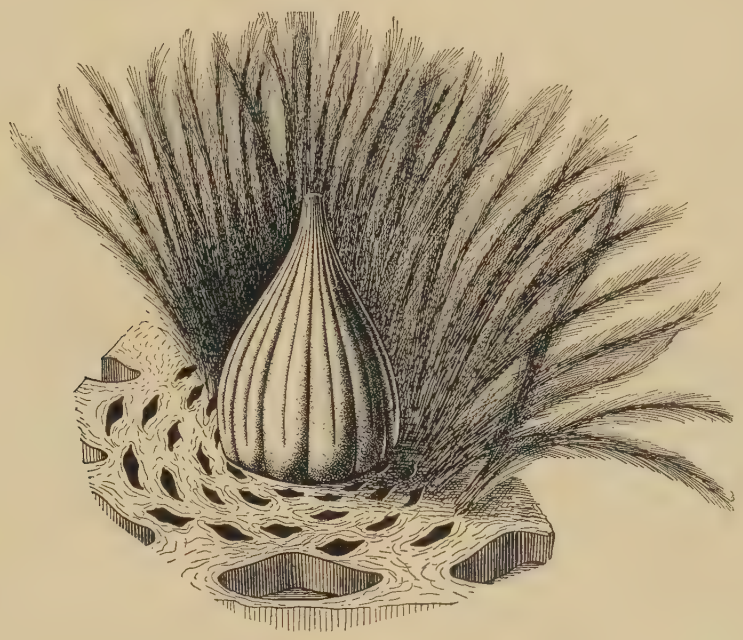


FIG. 21.—Restoration of medium-sized flower bud of the *Cycadeoidea colossalis* or *C. Marshiana* type at time of pollen maturation, with bracts partly removed.

Cycadeoidea McBridei Ward.

1893. *Bennettites dacotensis*, Macbride, in part. Am. Geol., Vol. XII, p. 249, Pl. XI, Fig. 2; Bull. Lab. Hist. State Univ. of Iowa, Vol. II, No. 4, pp. 391–392, Pl. XII, Fig. 2.
1894. *Cycadeoidea dacotensis* (Macbride), Ward, in part. Proc. Biol. Soc. Washington, Vol. IX, p. 86.
1899. *Cycadeoidea McBridei*, Ward. Ann. Rep. U. S. Geol. Surv., XIX, pp. 612–615, Pls. XCI–C.
1900. *Cycadeoidea McBridei*, Ward. Am. Jour. Sci., Nov., p. 392.
1906. *Cycadeoidea Macbridei*, Wieland. American Fossil Cycads, Vol. I, p. 63, Fig. 33, 4, Pl. VI, photograph 2.
1911. *Cycadeoidea Macbridei*, Wieland. Am. Jour. Sci., Vol. XXXII, pp. 143, 148, 150.

At the same time that Professor Macbride figured the original type of *Cycadeoidea dacotensis* he gave as a supplementary illustration the photograph in natural size of a portion of the lateral surface of one of the two score trunks which he had collected under the impression that all represented one and the same species. Later, when Professor Ward came to study the series of Minnekahta specimens in the U. S. National Museum, he decided from the figures first published in the *American Geologist* that the armor illustration indicated an additional species, which he named for Professor Macbride but wrote *Cycadeoidea McBridei* because of a typographical error which appeared at one point only in the original description. Unfortunately the laws of nomenclature and priority prevent the correction of such misspellings. The trunk of Macbride's Plate XII, Figure 2 (165*a*), is not a *C. dacotensis*.

It is too early to say just what trunks are to be included in *Cycadeoidea McBridei*. I have seen the original type, but not until both it and the type of *C. dacotensis* have been sectioned will anybody be in a position to determine the true relation of these two initial species. It is certain that among the State University of Iowa trunks there is a second

species of more or less columnar habit with small ovulate cones very nearly resembling those of *Cycadeoidea Wielandi*, but characterized by much larger leaf bases. As already explained, trunk 131 of the Yale collection may possibly be a *C. McBridei*, and in my preliminary paper on seed structure (1911) I so called the seeds of this trunk. However this may be, the various specimens from first to last referred to the present species by Professor Ward give us a fair conception of what he regarded as its average or general features. And he was consistent in referring the Yale trunk No. 8 to *C. McBridei* as he understood it. This specimen is probably of the same species as trunk 131, with which it closely agrees in general proportions, the large size of its leaf bases—much larger than in either *C. Wielandi* or yet *C. Dartoni*—as well as in the thick cortex, the form of the ovulate cones, and the structure of the seed coats.

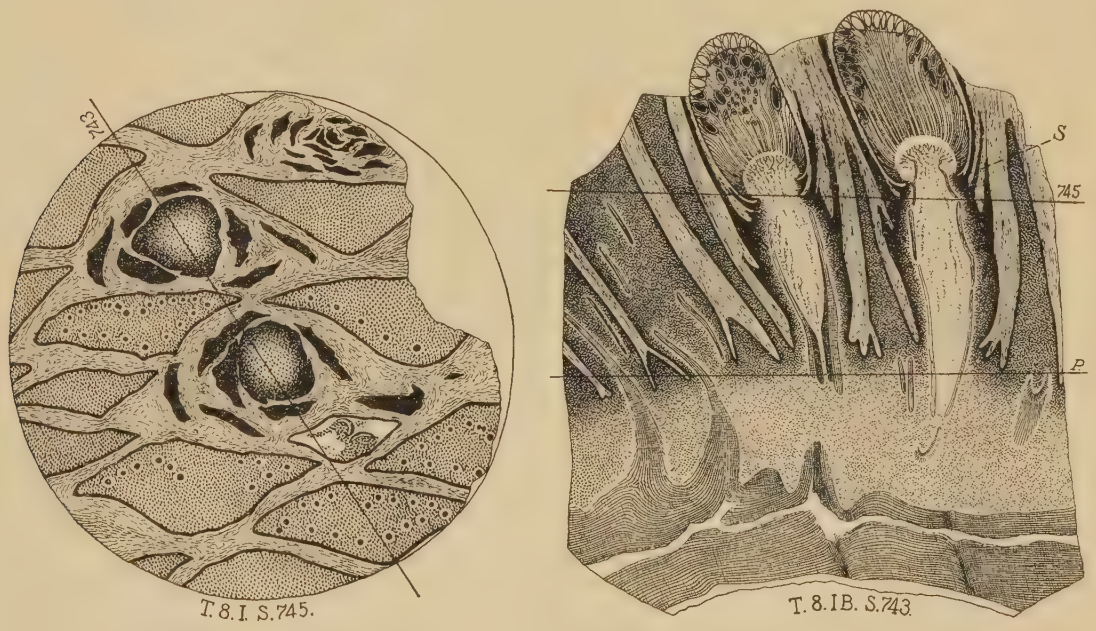


FIG. 22.—*Cycadeoidea McBridei*. Yale trunk No. 8. Longitudinal and transverse sections through a cylindrical core containing two adjacent very nearly superposed ovulate cones and one lesser axis.

These two sections show all the characteristic features of the armor, cortex, and woody cylinder. P in the longitudinal section 743 marks the plane of a polished transverse surface cut through the outermost cortex but not drawn. The line marked 745 is intended to mark the plane of the section so numbered and here illustrated, but is not placed with sufficient accuracy, as the peduncles are cut very nearly in the true transverse, instead of a quite oblique direction. Both sections are shown slightly reduced (about nine-tenths natural size).

Figure 22 represents in the natural size the longitudinal and transverse sections of a cylindrical core which extends to the medulla of Yale trunk No. 8, and will afford a sure basis of comparison when similar sections are cut from the crucial types. But until such sections are available it is not necessary to even provisionally transfer trunk 131 to the present heading, as I have been somewhat inclined to do; and it suffices to add that in addition to the supposed State University of Iowa type and trunks 8 and 14 of the U. S. National Museum collection, Professor Ward attaches the following numbers of the Yale collection:

8,	38,	180,	233?,	258??,	298,	325,	343?,	381,	422,	449,	472,	496,
19,	42?,	189?,	235,	262,	299,	326?,	346?,	383?,	429,	456,	489?,	497?,
23,	46,	225?,	245,	268?,	301?,	329?,	361?,	387?,	431,	462?,	490,	522?,
26?,	73,	227,	250,	271?,	305,	338?,	375,	388,	436?,	467,	492,	544?,
27,	76,	228??,	252,	288,	314?,	339?,	379,	407,	437,	469?,	494,	
29??,	179,	231,	257?,	289,	320?,	340,	380,	415,	439?,	471,	495?,	

It is of further interest to observe that aside from the questions that can be determined only after some further study of histological features, the present conception of *C. McBridei* is that of a trunk with very regular leaf-base spirals of larger size than in *C. dacotensis*. But it will generally be found that the *C. McBridei* specimens are basal segments of trunks in which, as the result of a certain amount of leaf-base excision in life, if not in part actual weathering subsequent to fossilization, the ramentum is less, the leaf bases more prominent. Moreover, in just such basal segments representing the young and vigorous stage of trunk growth few scale leaves are present, it being quite certain that some of the summits pertaining to these very segments must appear very different because of the presence of copious ramentum and numerous scale-leaf bases little subjected to excision by advancing periderm before fossilization. The great abundance of scale leaves in the Cycadeoids was not understood until recently. In Volume I it is stated that such must be present, but tangential sections covering large areas of trunks like those illustrated on Plates X and XI were not then available, so that it was not seen that scale leaves so generally characterized certain species; in fact it still appears that, as in the existing *Macrozamia spiralis*, no scale leaves were present in such Cycadeoids as *C. rhombica* and *C. formosa*. It now seems evident that, as forms like *C. Dartoni* and various of the types referred to *C. McBridei* approached the period of free production of fruits or of culminant fructification, there was a distinct cessation of normal frond growth, and that along with food storage there was a certain further economy in the early development of a compact and heavy growth of summit-protecting bracts and ramentum, permitting also the emergence and increase in size of the embedded fruits far more readily than would the heavy and rigid leaf bases. Indeed, it is exactly these studies of plain requirements of space for fruit growth and likewise protection of the cones that go so far to simplify our conceptions of those really ordinary structures which give to the Cycadeoids a strange appearance. To enter into any fuller discussion of general features is unnecessary here, but it is plain that the mass of ramentum which enveloped the trunk summit, and was in most forms abundant far down on the sides of the trunks, not only afforded protection to the cones, but may have greatly favored cross-fertilization by holding at the right season of the year any needed abundance of water. In other cases it may be that the staminate disk with its heavy woody dome was held in place for a time after dehiscence, while (as in *Cephalotaxus*) the seeds may have exuded drops of liquid at the time of fertilization, or some water could have entered to form the menstruum for free-swimming antherozoids needed to secure a most perfect close-fertilization.

It is therefore shown that the scale leaves of the silicified trunks are of very considerable interest in bearing a slightly different relation to growth and development than did the *Cycadolepis* scales or the various forms of scale leaves which clothed the long internodes between the whorls of foliage leaves of the *Williamsonia* stems.

Cycadeoidea colossalis Ward.

(Figs. 23–28; also *cf.* Pl. XIV and Pl. V, Vol. I.)

1899. WARD. Ann. Rep. U. S. Geol. Surv., XIX, Pt. II, pp. 603–605, Pls. LXVII–LXXII.
1906. WIELAND. American Fossil Cycads, Vol. I, pp. 7, 52, 98, 99, 104; also Pl. V, Phot. 3 (not *C. Marshiana*).
1914. WIELAND. Am. Jour. Sci., Vol. XXXVIII, pp. 121, *et seq.*

No one who has visited the United States National Museum and examined, even in the most casual manner, the wonderful group of Cycadeoidean types there exhibited can ever forget the massive and marvelously conserved trunk called *Cycadeoidea colossalis*. But unfortunately the impressive perfection of this specimen, just as in the case of *Cycadeoidea dacotensis*, has thus far prevented histologic study and virtually robbed it of all definite

value in determining the species and growth stages actually present in the Minnekahta series. For sections of fruits, young branches, crown leaves, scale leaves, adventitious leaves, leaf bases, and wood zones all fail in both instances. Doubtless, however, both these types can be duplicated. The specimen figured on Plate V, photograph 3, Volume I, can not be a *C. Marshiana* as there named, and now appears to be a lesser trunk of identically the same species and much the same stage of fructification as the National Museum *C. colossalis* type. As reference to the plate cited shows, the Yale specimen is made up of three original numbers, 13, 17, and 40; but the fact that these segments make up a complete trunk was not determined until after Professor Ward's preliminary study of the Yale collections accumulated up to the year 1899. The three fragments join on fracture lines distinctly visible in the photograph, and solely because of the bearing on the value of *macroscopic* types (!) the fact may be recorded that the segments 17 and 40, which are basal and weigh 65 and 64 kg., respectively, were referred by Professor Ward to the species *C. colossalis*, but the apical segment, which weighs 21 kg. was referred to *C. dacotensis!*

A Cycadeoidean trunk which can not be sectioned because of segregation for exhibition purposes does not, in justice to the investigator, constitute a valid type and is just as much the basis of a *nomen nudum* as an unfigured and undescribed fossil of any kind to which a specific name has been arbitrarily attached. As related in Chapter III, Volume I, it is a simple procedure to drill a cylindrical core from any of these trunks; and, moreover, the interest of any and all of them is in every respect increased by cutting and bringing into view the entire longitudinal and transverse trunk sections. It is accordingly necessary to state in self-defense that throughout the study of the American fossil cycads a persistent effort has been made to investigate first of all the types of most interest. In the case of *C. colossalis* no decision has been reached and it is only possible at present to give some further notes and comparisons of external features and to supplement these notes with descriptions of the highly interesting isolated flower bud and leaf base which follow.

ISOLATED FLOWER BUDS.

As every one knows who has examined at all attentively the Yale, State University of Iowa, or National Museum collections of Cycadeoideans, or the long series of silicified trunks which from first to last has been obtained from Italy and from the Isle of Portland, the number of fruits of larger size preserved in entirety is very small. The tendency is for the fruits to be broken away—entirely where the peduncles were of some length, or partly where the fruit, though borne on a shorter peduncle, reaches any considerable size. Moreover, on studying those lesser fruits which appear to be wholly enveloped by ramentum, a considerable number prove to be very young; others, a very large number, are found to be young ovulate cones; while a far from inconsiderable number of the axes are found to contain cavities lined irregularly by quartz druses, or to have their tissues broken down. Again, there is much difficulty of fruit study in the case of many important trunks, due to that natural dislike that an investigator must have, to a certain extent, of injuring a great specimen by cutting away one or two fruits instead of studying it systematically after sawing through it longitudinally and obtaining the segments most favorable for completer study—an operation requiring time and resources. Also, the number of conserved disks being at best but small in proportion to the ovulate cones, knowledge of the staminate disk variations in form and structure has accumulated relatively slow.

It thus transpired that, as related in Part VI of the preliminary studies (393), the very reduced size of some of the flower buds of relatively large trunks long remained a rather hidden character, although small and young fruits were among the first of the subjects

considered important and to which much attention was given. Inasmuch as the general characters of the trunks indicate marked specific variety, it has not been at any time a source of surprise to find considerable variation in the size of the disks and the number of microsporophylls composing them.

In the flower type here considered, however, there is an added interest, not only because of the large amount of reduction in the fertile segments, both ovulate and microsporangiate, but especially because of the great relative bulk of the microsporophylls and their very peculiar form. The features are, moreover, of importance in criticizing previous restorations where the apical region is less complete. Not only so, but the restorations given are suggestive of certain larger and undeniably sigificant hypotheses as to the true nature of both ovulate and microsporangiate floral structure, which are considered at length in the chapter on seeds.

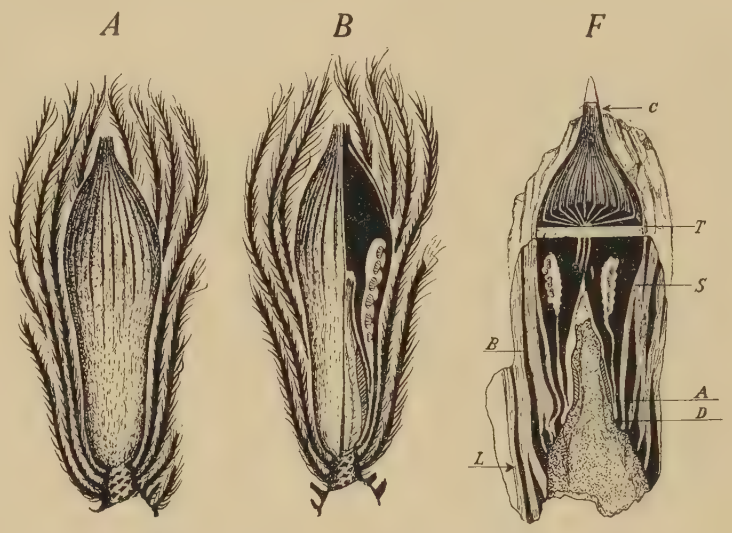


FIG. 23.—*Cycadeoidea colossalis.* Drawings showing external and structural features of the bisporangiate flower bud with enveloping bracts indicated diagrammatically. About natural size.

A. Exterior view of bud, in part diagrammatic and drawn in approximate proportions, the base being somewhat narrow. Note resemblance to so-called *Neuropteris* seeds in both form and surface grooving.

B. Same as preceding, with one-quarter of fruit bud cut away to bring to view central ovulate cone and synangial region.

F. Drawing of longitudinal section through flower-bud extending up to plane (*T*) of trial section and surmounted by dome-shaped apex of disk (*C*), which is drawn in full relief, just as it appears after splitting away a portion of the bract husk.—*C*, dome formed by extension of paired and closely appressed rachidal appendages; *T*, plane of trial section (Fig. 1); *S*, synangia; *A*, decurved tip of staminate frond extending just to base of the ovulate zone of the central seed cone, which is shown relatively large, being very young and small; *D*, disk insertion; *B*, *L*, outer bracts next to leaf base.

While preparing material for Volume I there was noted as a specimen of especial interest an upper portion of a trunk of the Yale Collection numbered 549+550. A half dozen or more medium-sized flower buds enveloped by large bract groups, and the distinctly rhombic-shaped leaf scars of lesser to small size, were the particular features which arrested attention. In general, the characters suggested *C. dacotensis*, to which species Professor Ward had indeed referred both these trunk fragments, later found to fit together as a single large more or less apical segment of a trunk or perhaps branch. But the lesser variations led to the sectioning of one of the flowers, which, although it proved to be indifferently conserved, indicated the structureless outlines or casts of the microsporophylls to be remarkably heavy and thick in the apical region of the disk. However, as the single section cut so lacked finer structural detail, little could be said about the floral features, while on examining several other of the axes, exteriorly more promising, nothing further was learned of the structures present. As is often the case in the fossil cycads, petrification had resulted in the replacement of the original tissue by silica in much too granular to quartzose a condition for the clear preservation of histologic details. The further study of this specimen was therefore deferred, and attention was not again directed to it until much later, when the sections shown in Figure 23, *F*, and in Plate 57, photographs 2, 3, were cut from an isolated flower-bud collected at Minnekahta

in the autumn of 1902. This flower bud has a complete summit and at once recalled the trunk apex and section just mentioned; for so nearly alike are the general features and the type of conservation that it is not impossible that the isolated fruit really pertained to the two larger trunk fragments and escaped attention when they were collected some two years earlier at the same locality. My own search for new material was, of course, carried out with far more care than that of the earlier collectors, who, quite without exception, had mainly sought huge or otherwise striking specimens.

SPECIFIC POSITION OF SPECIMENS.

Doubtless the isolated flower bud and the trunk summit under consideration must both be placed in the same species. Furthermore, both may be provisionally referred to the same species as the great type *Cycadeoidea colossalis* of the U. S. National Museum. In the original descriptions of this specimen no very clear distinction from the prototype of the Minnekahta series of species, *Cycadeoidea dacotensis*, is definitely pointed out. But a close reading of the measurements shows that the leaf bases are very small and the floral axes of only medium size. In *C. dacotensis* the lateral and vertical diagonals through the leaf bases measure from 16 to 26 mm. and 10 to 16 mm., respectively, as compared with 13 to 16 mm. and 8 to 12 mm. in the *C. colossalis*. This is a really striking difference, when it is recalled that the largest of the trunks or branches definitely proven to belong to *Cycadeoidea dacotensis* weighs a scant 100 kg., whereas the great National Museum type exceeds 300 kg. in weight, being one of the largest single stems, if not "the largest," in the world. The huge columnar trunk of the Yale Collection, *C. ingens*, which yielded the first flower buds with disk features studied, has the greatest recorded weight, 303.91 kg.,* and after it comes the famous Dresden trunk *Cycadeoidea Reichenbachiana*. The largest known single branch is the superb specimen shown in Plate V, Figure 1, Volume I, with a weight of 147 kg., and the greatest weight yet determined in a branching aggregate is 844 pounds (383 kg.), seen in the group figured in Volume I, Plates XII and XIII.

No further facts need be given to show that the type of *C. colossalis* has distinctive features, even in the absence of the closer knowledge of its actual woody cylinder and other of the more searching details of trunk structure so much to be desired; nor is it necessary to enumerate other forms related to *C. colossalis* and show how they differ in first one, then another, of the known features.

With respect to the floral structures of the type of *C. colossalis*, we are as yet largely in ignorance, but there is some indication that these also will be found of essentially the type here described. Just as in the case of the Yale trunk fragment and the isolated fruit now considered, the flower buds are of slightly lesser size than in *C. dacotensis*, but have an enormous development of the bracts, the outer of which even closely approach in size the relatively small leaf bases. It is, therefore, with considerable confidence that future closer study may fully justify the provisional reference of these Yale Museum specimens to *Cycadeoidea colossalis*, that their very singular floral features are again recorded under that species.

DESCRIPTION OF STRUCTURE.

The preservation of structures as indicated by the sections so far cut from the above-mentioned isolated bisporangiate axis is very uneven, but yields the details affording the restoration given in Figure 25. An attached leaf base, however, very fortunately shows

*In the late autumn of the year 1898 I re-examined the exact spot where *C. ingens* was collected (*cf.* Vol. I, Pl. XLIX, upper figure), finding a few additional fragments from the apex of the trunk, increasing the weight of this great type to over 304 kg.

remarkably fine preservation of structure, some of the bundles clearly showing all details and possessing more development of enveloping sclerenchyma than has been seen in any other American specimen. Also an occasional bract is well conserved, and the appearance of the material from which supplementary sections remain to be cut indicates that considerable further structural details may yet be observed. The leaf-base bundles and the plan and form of the flower alone are described.

The first or trial section cut from the isolated bud was that drawn in Figure 24. It clearly shows the characteristic small size and lozenge-shaped transverse section of the nearest adjacent leaf base well crowded to the side by the series of relatively very large bracts. The outer bracts appear the larger because cut at a much higher level than those next the essential organs, the bracts being slender near their insertion and increasing in size toward and beyond their mid-length. As they are still large where truncated by the eroded outer surface of the fossil, about a centimeter above the level of the trial section, the actual terminations, as in most fair-sized fruits, can not be observed. It is nevertheless clear enough that the bracts were long and heavy and formed a dense protecting husk gracefully closing in over the apex of the shapely dome. At the center of the bract series, as one notes in Figure 24, only the disk features may be seen, since the section is cut well above the apex of the ovulate cone and also passes above the highest of the synangia. All the tissues cut at this level, which was intended to and actually does traverse the broadest part of the flower bud, are therefore rachidal; and furthermore, as one attentively studies the section, it is plainly seen that the closely appressed and transversely cut rachides have the appearance of a series of heavy V's with their sides close together and their vertices outlining a very small circle or point near the center of the flower, except that in several instances the arms of the V's barely touch at the center, while in one case the V section of a rachis is seen to unite near the inner or vertical point with the arm of the adjoining rachis, the other arm of which is thus left entirely free. But at the center there is not the least trace of the decurved tips of fronds clearly observable in the longitudinal and more basal transverse sections, so that there can be no mistaking the fact that this entire section shows only the development of the heavy rachides. Obviously enough, therefore, the series of sector-like rachidal sections pairing into, as one may readily count, ten V's with arms mostly joined but sometimes free, or again fused with an adjacent member, indicates one of two possibilities: either the disk divides irregularly into outer or ventral wing-like expansions of the rachides, the number of which would in this case be somewhat uncertain, or it divides at quite exactly the level of this section into ten distinct rachides, each of which is deeply incised by a median ventral furrow so as to form normally twenty divisions at the summit of the flower. This latter is the true structure, which must be fully confirmed by any further sections, although there are some slight departures from entire symmetry of form.

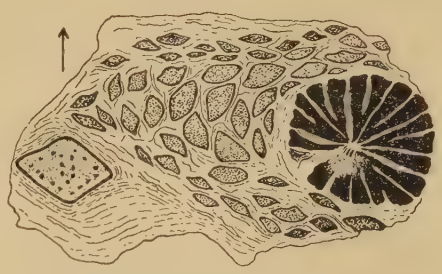


FIG. 24.—*Cycadeoidea colossalis.* ×1.
Section through dome of disk just at level at which the ceratoid appendages divide.

The presence of outer median rachidal furrows has already been noted in the very different flower of *Cycadeoidea Marshiana*. This latter, however, is a much smaller species of flower and the microsporophyll surfaces are much more crinkled and rugose, while the apex is not present. But a small median furrow traverses the outer or ventral face of each rachis, as Figure 16 indicates. Evidently the depth increases toward the apex.

Failing the deep incision now observed, the full significance of that small notch was by no means at first appreciated, though it could not escape observation when the drawings were made. As reference to the figures shows, the groove was only seen near its lower and shallower end at a height of a full centimeter or more above the central cone. Fortunately, all the upper portion of the bud before us is present, save a very small, slender tip, and the bracts are so broken away on one side as to disclose the entire outline of the bract-enveloped disk apex, which rises in the form of a symmetrical spired dome.

With the trial section just described completed, it was possible to locate and cut to the best possible advantage the supplementary longitudinal section. This, as drawn in Figure 23 in conjunction with the view of the dome-shaped summit, yields nearly all further larger details of the floral structure and plan. It brings to view the very heavy bracts, somewhat irregularly appressed in position, the large peduncle and ovulate cone of inverted pear-shape with a very minute and limited seed zone, the exact thickness of the disk and its insertion, the decurved microsporophyll tips, and finally the rather limited fertile or synangia-bearing space, with the immense expansion of the sterile rachidal region just at the base of the terminal dome. Special features are the relative narrowness of the seed zone, to the basal portion of which the microsporophyll tips exactly reach as a complete inclosing curtain, and the high position of the synangial region above the fertile zone of the seed. This latter feature is partly paralleled in *C. Marshiana*, but quite different from the condition seen in *C. dacotensis*, where the synangia grow far down in the campanula toward the base of the ovulate strobilus.

FIG. 25.—*Cycadeoidea colossalis.*

A series of about natural-sized but wholly arbitrary restorations of fruit shown in the preceding drawings, given for the purpose of further bringing to view the flower-bud structure as it might appear were such a flower freely expanded.

The pen sketches of Figure 25 may aid in visualizing the floral features and plan. A generalized drawing of the trial section is introduced to show the ten V-shaped transverse sections of rachides as cut at base of the terminal dome. The level of this section is indicated by the arrow near the summit of the flower arbitrarily shown in expanded form, but with half of the axis cut away. In all the sketches the seed zone and synangial region are represented much above the proportionate size, while the peduncle appears relatively small, the object being merely to bring sharply into view special features rather than to give a final restoration. With regard to improbability of expansion of the dome-forming disk see the succeeding paragraph.

COMPARISON WITH OTHER CYCADEOIDEAN FLOWER-BUDS.

This is indeed a flower of singular aspect. And it is safe to say that the prolongation of the sterile spinose pairs of median rachidal wings into a dome-like expansion, not only taking up all the space between the outer husk of bracts but carrying them up as a high summit, would never have been suspected without actual observation. The long bush of

terminal sterile scales visible in most ovulate cones with the elongate type of cushion easily led to the belief that the ovulate cone formed a summit above the always decurved microsporophylls and thus took up any unfilled space between the fertile organs and the bracts rather than that any open tent-shaped space was left between these organs and the floral envelope of hairy bracts. The casts of *Williamsonia gigas* figured by Williamson seemed to lend further support to such explanation of the outer form, which, it may well prove, is partly or wholly correct in the case of some species. However this may be, it is only the actual evidence to which one may turn. In the case of *Cycadeoidea ingens* nearly the entire flower is present, and in the original description the radial structure which appeared very vaguely at the summit was observed and the fruit rather happily termed a "capsular male fructification." But it was then thought that, as the summit was quite small, only a few millimeters could have been eroded away, which if true would leave the restoration essentially correct as given. Now it seems probable that a dome was present; though it is not to be overlooked that this may have been *rounded*, not *spired*, in which case the restorations first given are essentially correct.

The case of *Cycadeoidea dacotensis* is more doubtful. It might have had a greater or a smaller dome than the *C. ingens* (see Vol. I, Plate II), or none. The huge rounded and wholly bract-covered fruits of the original type in the State University of Iowa collection must be ovulate cones from which the staminate disks have been shed. Those with disks end roughly and are thus partly eroded at the summit. It is clear at least that if, as first supposed, the ovulate cone is much elongated no dome can be present. So far the apical region of a well-preserved flower of *Cycadeoidea dacotensis* has never been seen; but now that the subject has assumed such a tangible interest, the actual dome structure will be searched out and studied. If the flower really had a dome it must have appeared much as arbitrarily shown in longitudinal section in the adjoining Figure 26.

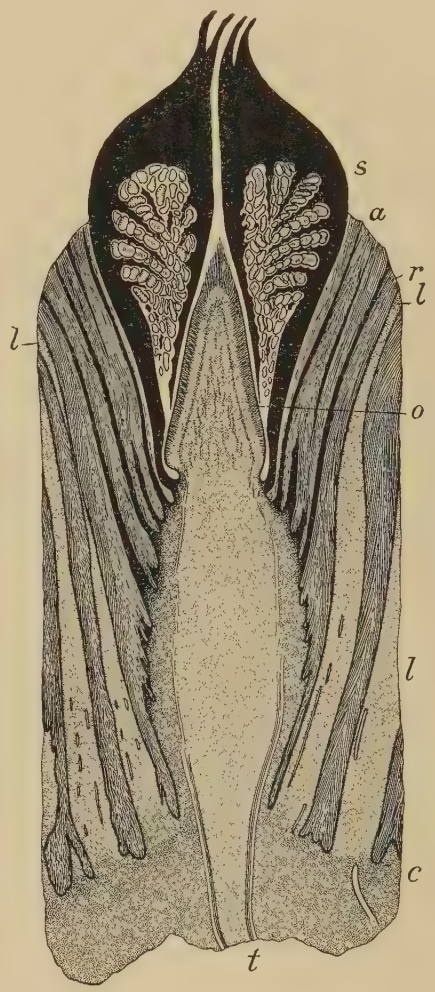


FIG. 26.—*Cycadeoidea dacotensis.*

Median longitudinal section through amphisporangiate flower bud terminated arbitrarily as a dome of spurs not essentially different from the megasporophyll horns of *Ceratozamia*. For interpretation first given with reference to original sections and lettering, see Volume I, Figure 71. About three-fourths the average size, or only half the size of the very largest examples.

In *C. Marshiana*, as described, the flower is very small, and so far the disk apices have not been noted. The figures given show structure only and are all absolutely correct in all details, so that anyone may judge for himself as to whether there was development of a dome. It seems quite certain that there was a distinct dome to that flower.

LEAF-BASE BUNDLES.

The same trunk fragment which yielded the domed bisporangiate flower-bud illustrated on Plate 58 contains several leaf bases in which the bundle features are conserved in remarkably clear detail. In fact, it is on the basis of the great development of the bract husk and

on the leaf-base form that ascription to *Cycadeoidea colossalis* is provisionally made. For the present, however, the main point of interest is the anatomy of these bundles, taken as a characteristic type for the Cycadeoids. Text-figure 27 is a drawing of one of these bundles by Miss Lisbeth Krause, based on a photomicrograph blueprint and worked out with constant attention to details. A better drawing of the bundle as it appears under the microscope could not well be made in black and white. Fig. 28 shows the average conservation.

This bundle can be better described than lettered, taking as a starting-point the protoxylem region (*pr*) and the more or less crushed phloem (*cp*) bounding the outer limit of the centrifugal xylem. Between these two points the centrifugal xylem stretches out like a broad fan, just as in existing cycads, the tracheid and parenchyma rays, each one cell thick, tending to alternate regularly. Distal to the crushed phloem the main mass of the phloem contains many sclerotized elements, merging into a pronounced ensheathing tissue which continues more or less definitely all around the bundle. If in the drawing the inner limits of this sheathing sclerenchyma are uncertain, this is only because the same uncertainty appears when studying the bundles themselves under the microscope. But the really debatable bundle region is that occupied by the prominent group of large tracheid-like cells occupying the centripetal xylem position, assuming these bundles to be truly mesarch as in the existing cycads. These elements are quite prominent in *Bennettites Gibsonianus*, where the leaf-base bundles are conserved in marvelous perfection. Whether or not they are short, as Dr. Scott once suggested might be the fact, is still uncertain; such silicified plant tissues are very variable indeed in the conservation of histologic details. Thus, in the leaf-base section which yielded the bundle drawing just described, no other bundle is wholly complete, and this of course means that, aside from the slight chance of cutting any one bundle in the true radial longitudinal position, there are in every bundle long and irregular structureless gaps. Then again, in trunk after trunk, over all the areas studied, in even the largest of sections, the bundle structures are much too imperfectly conserved to yield ultimate structural details. Nevertheless, as was suggested in the case of the micropylar tubes, material may any day be cut yielding detail on detail in an absolutely conclusive profusion.

FIG. 27.—*Cycadeoidea colossalis.* Transverse section through leaf-base bundle of outer armor. *pr*, protoxylem; *cp*, the crushed phloem parenchyma. ×140.

To repeat, the type of bundle here figured is the characteristic one for the Cycadeoideas, although varying markedly in the different species in the amount of sclerenchyma present and in the prominence of the centripetal xylem, so called. This in some forms is limited to

a single cell or two, or may even be absent, perhaps in bundles of some certain situation. The manner in which this region of the bundle may vary remains undetermined, though as the cortex is approached the centrifugal wood only is noted, the bundles increasing rapidly in size as they coalesce into the two main bundles which then unite to form the U, or horseshoe, cortical trace. Compare with figure 34.

NOTE ON THE UNITED STATES NATIONAL MUSEUM TYPE.

Following the preparation of the foregoing notes, the surface features of the great National Museum type were once more scanned with care, point by point. The columnar trunk is but slightly flattened and such lesser or incipient branches as may be present are scarcely distinguishable from the fruit axes surrounded by enormous bract groups. The specimen is, however, even more remarkable for its conservation than for its huge size and symmetry. The more attentively the surface details are studied the more is one struck by the absence of fractures and by the fine conservation of every detail. The solidity of texture and the nearly black color add almost the last possible touch of perfection.

As a first result of surface study, however, the identity of the floral type just described appears less certain. One side of the specimen is slightly lime-coated and must be even more perfect than the side figured by Ward on his Plate LXVII (357). Near the edge of this coated side and towards the apex of the trunk a young staminate flower may be distinguished which appears very much like the form figured above in both size and bract development, but probably has from five to six more stamens. Amongst the three score or more fruit axes present there must be a number of these staminate disks in excellent preservation, but any such are uniformly covered over by the bract groups.

FIG. 28.—*Cycadeoidea colossalis.* ×100.

Transverse section photomicrograph of bundle from same leaf base as that of the preceding pen drawing. Both the protoxylem and central phloem fall in imperfectly conserved areas in this bundle.

It is accordingly worth while to present the argument for preserving such an unusual type intact and foregoing indefinitely the results of sectioning. Unquestionably the two main elements of doubt which prevent a positive answer one way or the other as to whether such specimens should be cut are, first, the question as to whether cutting methods have reached a sufficiently high degree of precision; secondly, the likelihood of obtaining other equally fine specimens as the years go by. It would have been an error to cut the great *Cycadeoidea Reichenbachiana* when first reposed in the Zwinger Museum, but it is fair to say that it was an error not to cut the specimen from the time of Sorby and Witham down to the present day. It remains an error which, as pointed out in the notes on the Dresden specimen, has been a distinct disadvantage not merely to German students but to botany. The discovery of the American series has not removed the need for sectioning. It has merely made such work historically less important. Similarly the failure of English students to section

the Buckland types *Cycadeoidea megalophylla* and *C. microphylla* has been the main cause of tangling in the nomenclature of the silicified trunks. In this instance, however, it could hardly be pleaded that the purpose was to conserve the types, since these have not been seen in recent years, although it is to be hoped they are not permanently lost to view. Very different was the method pursued in the case of the great Yale type *Cycadeoidea ingens*, with results which are now a central chapter in the history of Cycadeoid study. Needless to say, very few who ever visit the Yale Museum will note the absence of the trunk portions removed for study by far more summary methods than those now available. And in this connection it will be of interest to botanists to learn that absolutely the handsomest trunk in the Yale collections, No. 54, as figured by Ward on Plates LXIV and LXV of the Nineteenth Annual Report of the U. S. Geological Survey, was some time since removed from its elegant exhibition base for sectioning and the most thorough study possible to modern methods.

Evidently, as the course of future discovery goes on, each new specimen of unusual beauty or of somewhat compelling and defying proportions will, as in the past, seem to afford a reason for setting aside direct methods of study, while the value attached to knowing the exact fruiting stage of an initial type of course depends on the individual point of view. It may assuredly be said that it is better to make haste a little more slowly in the structural study while there is hope that erosion in the region about the Black Hills may give the clue to other and quite as wonderful groups of trunks as have been found in the past, to say nothing of the possibilities of excavation on an adequate scale at the older localities. Doubtless, too, it can be urged that in the course of time, it will be possible to give to the study of the duplicate series of Cycadeoids all that quantitative as well as qualitative value necessary to meet the most stringent demands of the stratigrapher; for it scarcely seems possible that the several groups of these highly organized plants can fail as horizon markers, however persistent some of the species may prove to be. Hardly the competent scientific method, hardly an achieving attitude of mind.

Cycadeoidea nana Ward.

1899. WARD. Ann. Rep. U. S. Geol. Surv., XIX, pp. 639–641, Pls. CLVI, CLVII.
1912. WIELAND. Am. Jour. Sci., Vol. XXXIII, pp. 87–89, Fig. 10.

Yale specimen No. 84, made by Professor Ward the type of a species of rather doubtful status, is a handsome flattened globose small trunk or branch with unusually small leaf bases producing a very characteristic armor. The height of the specimen is 12 cm., with a diameter of 15 by 17 cm. The presence of a few lateral buds, apparently of young fruits, in the case not only of the type No. 84, but occasional other specimens of more or less similar aspect, has led to the impression that there is actually present at Minnekahta a fairly well-represented group of pygmic trunks, which are essentially mature forms and should be justly brought together as a much-branched group, conveniently placed under the present heading. Without considerable section-making it would, assuming that this group is rightly founded, be very difficult to separate from it with entire precision juvenile forms of other and much larger species. However, in a given series the leaf bases of such young trunks must very soon reach a large size; only while the plant is small and bulbous are the fronds relatively small.

In the first place, the trunk illustrated on Plate 38 is of very especial interest as a small and freely branched Cycadeoid bearing various young fruits and at least one ovulate cone well enough advanced to be of distinct help in establishing the species. It has, more-

over, an added importance as one of the few trunks from the Black Hills found undisturbed *in situ*, having been discovered by the writer after days of patient search at the well-known Minnekahta locality in the summer of 1902. The specimen lay on its side wholly embedded in a characteristic stratum of straticulate clayey sandstone near the summit of the flat-topped hill about which most of the Minnekahta trunks were found. The great specimen of another species illustrated on Plate V, photograph 1, Volume I, was also collected from a point some distance further along this same slope several years earlier, having been likewise found in the *in situ* position as related in Volume I, pages 40, 41. (See fig. 14*a*.)

The size of the leaf bases of the Plate 38 specimen is about the same as in *Cycadeoidea Paynei*, although identity can in any event be determined only by later study. The next set of specimens which invites comparison is of course the *C. Marshiana* group. But these are excluded specifically because the ovulate cone has a conical parenchymatous cushion, which is not the case in the specimen before us. Fortunately a small ovulate cone about 1 cm. in diameter by 2 cm. in length borne near the summit of the main stem is well conserved, the sections revealing a flatly convex cushion; whence it appears that *C. dacotensis*, with the allied *C. superba*, *C. Marshiana*, and *C. nana*, include a clear succession of trunks passing from the largest of compactly branched forms to lesser and finally small-sized and small-flowered freely branched trunks. The floral indices of this trunk series are also fairly distinct, *C. dacotensis* having a huge disk of 17 or more fronds and *C. Marshiana* a much smaller flower with 11 or 12 fronds; while in *C. nana* the disk remains unknown, but the ovulate cone varies from that of both the foregoing species because of its convex instead of elongate parenchymatous cushion. It is of the greatest interest to observe, moreover, that a transition from the elongate to flat parenchymatous cushion is also indirectly indicated in the case of the series of great columnar trunks from the Piedmont-Black Hawk locality, as is brought out in the description of fructification in *Cycadeoidea Jenneyana*.

Cycadeoidea Wielandi (Ward).

1893. *Cycadeoidea Paynei*, Ward, in part. Proc. U. S. Nat. Mus., Vol. XXI, pp. 212–213 (quoad No. 77 of the Yale collection).
1899. *Cycadeoidea Wielandi*, Ward. 19th Ann. Rep. U. S. Geol. Surv., pp. 621–624, Pl. CXVI.
1899. *Cycadeoidea Wielandi*, Wieland. Am. Jour. Sci., Vol. VII, May, pp. 384–388, Pls. VIII, Figs. 1, 3, 56; Pl. IX, Figs. 8, 9, 10; Pl. X, Figs. 13–16.
1900. *Cycadeoidea Wielandi*, Wieland. Yale Sci. Mon., Mar., Pl. I, Fig. 6.
1900. *Cycadeoidea Wielandi*, Ward. Am. Jour. Sci., Vol. X, Nov., p. 33. (Enumerates Yale trunks 77, 131, 393, and 424 as representing this species.)
1906. *Cycadeoidea Wielandi*, Wieland. American Fossil Cycads, pp. 108–126, Figs. 23, 36–42, 58, 61; Pl. VI, Phots. 1, 6; Pls. XXI, XXII, XXIII, Phots. 4, 6, 7; Pl. XXIV, Phots. 1, 3, 4, 5; Pl. XXV, Phots. 4, 5, 6; Pls. XXVI, XXVII, Phots. 1–4; Pl. XXVIII, Phots. 1, 7; Pl. XXIX, Phots. 1, 3, 5, 6; Pl. XXX (with 4 figs. in legend); Pl. XXX 1, Phot. 1.
1911. *Cycadeoidea Wielandi*, Wieland. Am. Jour. Sci., Vol. XXII, Aug., Figs. 3, 4.

All of the specimens that have ever been described or discussed under the present species are located in the Yale Museum. In actuality this small group of trunks includes two distinct species, although it is not certain that either is represented in the National Museum or State University of Iowa collections. However this may be, in giving the above synonymy it has not seemed desirable to try to separate these species now, lest by so doing a certain amount of confusion might later arise. The simpler and better plan is to carefully characterize the several specimens, as will be done in the descriptions following.

The first of these included species is represented by the Yale trunks 77 and especially 393. These are given much prominence in Volume I, owing to their remarkably fine conservation and close agreement. No. 77 is the original type and No. 393 becomes the primary cotype; for it must still be assumed that these trunks vary specifically from the

unsectioned *C. Colei*, which antedates *C. Wielandi*. The *C. Colei* type is equally as well preserved as 393 and may be a broken-off branch of a larger clump, although Professor Ward looked upon it as simple-stemmed. It is, however, not so very likely that *C. Colei* includes either 77 and 393 or 131, and even less probable that *C. Paynei* could include either of these. Professor Ward was doubtless correct when he transferred trunk No. 77 from *C. Paynei*, to which species it was at first provisionally referred. Evidently a final decision on this point must await the sectioning of the National Museum type of *C. Colei*.

The second trunk type is represented by Yale specimen No. 131, rather arbitrarily, and as it turns out mistakenly, included here because it was observed to bear seed cones quite like those of trunk 77, which were the first to be studied and figured from America.

To get an excellent idea of the specific contrast afforded by trunk 131 and the two specimens 77 and 393, it is only necessary to refer to the illustrations of these trunks in Volume I. Reference especially to Plates XXI and XXII shows that while trunk 393 is of conical or more ovate form with small leaf bases, trunk 131 has larger leaf bases and a markedly columnar form. The leaf-base contrast becomes still more striking on reference to the plates of the present volume, the oblique section through the armor showing the bundle supplies of trunk 131 to have fully double the size seen in trunks 77 and 393, although the relative thickness and size of the woody cylinder is about the same in all three of these trunks. On this point compare Plate 29, photograph 1, with Plate 31, photograph 2.

A further and very interesting difference occurs in the seed cones and seed coats. The cones of trunks 77 and 393 agree in every particular. They are rather larger than those of trunk 131, and have larger and more numerous seeds, characterized, however, by the thinnest testa found in any *Cycadeoidea*. In fact, the thin-celled layer enveloping the middle stone is eliminated in nearly all the mid-region of the seed, whereas in the seeds of trunk No. 131 this outer layer is always quite pronounced. Even at low enlargements this difference is distinctly visible, as one may note on comparing the illustration of a cone of trunk 131, given on Plate XXII, photograph 2, with the photograph of a cone from trunk 77, Plate XXIII, photograph 6, of Volume I. Illustrations in the chapter on seeds further bring out this variation in the seed coats of these specimens. Very similar seeds and cones are present in the base of Yale trunk No. 8, referred by Professor Ward to his species *Cycadeoidea McBridei*. But considerable further comparison would have to be made before making any final pronouncement on this point or changing the several catalogues of species.

Leaving in abeyance for the present the exact specific boundaries of the small group of trunks catalogued as *C. Wielandi*, two very important rectifications of previous descriptions follow:

First, no mention of the presence of wood parenchyma in the woody cylinder of trunk 393 has hitherto been made. But Professor R. B. Thomson, on examining the sections made by the writer, at once called attention to the presence of wood parenchyma, also characteristic of the wood of the existing *Dion*, as described by Chamberlain. This is one more striking agreement in the structure of the fossil and existing cycads. It appears from the sections that the amount of wood parenchyma varies markedly in different regions of the trunk, this fact having partly caused the earlier insufficiency of description. To determine the proportion of wood parenchyma in the basal, mid, and apical trunk regions is one of many incompleted tasks of cycad study.

Secondly, in the earlier descriptions of fructification in trunks 77 and 393 it was stated that the proportion of younger fruits distributed among the full-grown seed cones was small, the inference being a strong one that such as were present might, in the ordinary

course of events, never have matured, and that a more or less monocarpic habitus was indicated. Naturally the first transverse sections cut through the armor were made for the purpose of displaying the features of the larger fruits, the lesser and younger fruits more deeply hidden in the armor appearing only in these sections more or less by accident. It was thus very easy, taking only the actual number of small fruits seen and counted, to reach the mistaken conclusion that the great majority of the fruits were mature. But the large and splendid transverse sections of the armor of trunk 393, made later and illustrated in the accompanying text-figures 30 and 31, show conclusively that the young fruits or aborted ovulate cones, if this indeed be their explanation, about equal in number the older cones. This fact, of course, has not only a bearing on the question of monocarpy, but on

FIG. 29.—*Cycadeoidea Wielandi*, type. Yale specimen No. 393. Polished transverse armor section photographed direct. About nine-tenths natural size.

In order to secure so large a surface without cutting fruits and leaf bases too obliquely, about the lower left third of the specimen is cut on a different angle, which accounts for the lighter color of this part of the illustration. The color values are very good, nearly reproducing the appearance of the polished surface, in which light nearly clear quartz incloses the very dark ground tissues of leaf bases, peduncles, and massed seed stems. An accurate drawing of the entire surface arbitrarily represented in a single plane follows as figure 31.

the even more highly interesting question as to whether these trunks were monœcious or diœcious. Because the central cones of the young or small fruits are more or less irregularly flat-topped and variant in form instead of round and regular as in trunk 131, but yet possess generality of type and have uniformly distinct traces of hypogynous disk insertion, it seems most likely that these flowers of the lesser series were bisexual, the ovulate cone being abortive and the plants monœcious and more or less truly monocarpic. Traces of disk insertion are, however, likewise present at the base of the larger ovulate cones, the alternative explanation that all the fruits, large and small, are bisexual and represent two successive seasons of fructification not being entirely excluded. It appears least likely that a functionally bisporangiate, or conversely a diœcious, condition is present; and it is, of course,

distinctly in favor of the view that a monœcious and monocarpic condition is indicated, to find in a much larger columnar trunk of the *C. excelsa* or *C. Jenneyana* form from the Black Hawk locality even more pronounced indications of the growth of pollen and seeds on separate axes of one and the same trunk, as described elsewhere. The sections on which these conclusions are based require detailed description, which follows.

DESCRIPTION OF ADDITIONAL SECTIONS FROM YALE TRUNKS 77, 393, AND 131.

Even in the study of the fossil cycads, a varied fruit growth can seldom be studied over such large areas as those represented by the serial sections of Figures 29 to 31. The single sections are interesting, the hidden features revealed by the complementary series doubly so. In fact, the interest and value of the series is much increased by close attention to position and feature. In the longitudinal section series, Figure 30, the base-line PS corresponds to

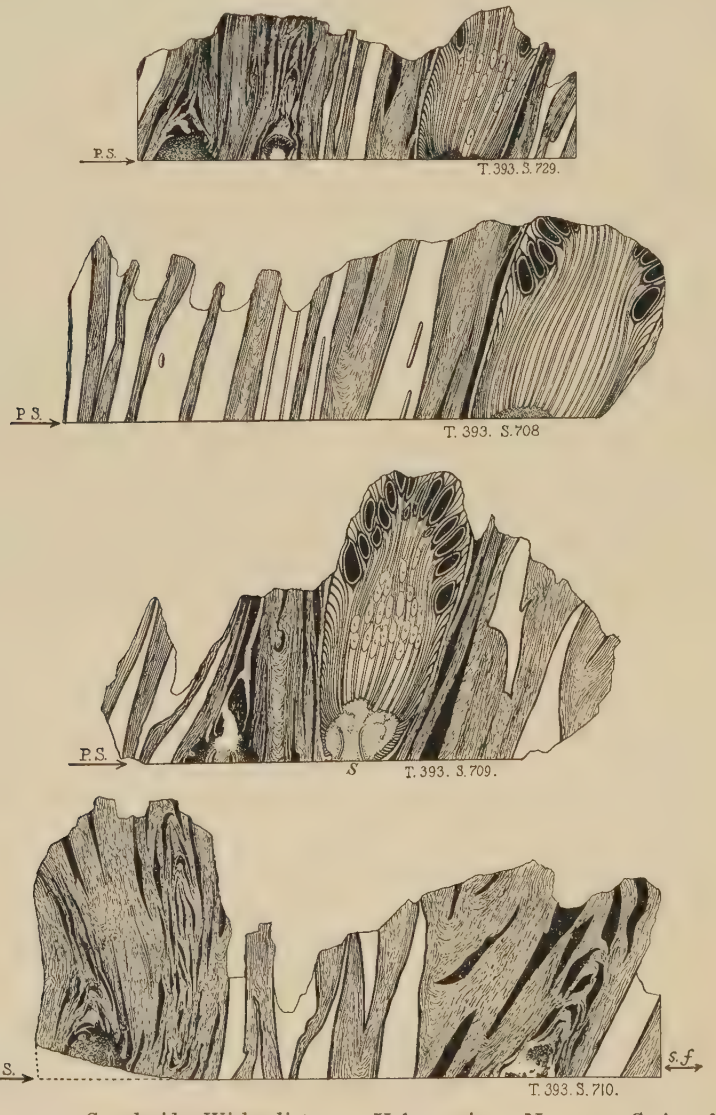


FIG. 30.—*Cycadeoidea Wielandi*, type. Yale specimen No. 393. Series of 4 parallel longitudinal sections through the slightly drooping armor cut in radial longitudinal trunk planes in positions indicated by the section numbers in succeeding figure, which see. All natural size.

the plane of the polished surface (Fig. 29), also Figure 31, where the exact positions are marked by number. The longitudinal sections are not quite so complete as the basal transverse section, some parts having been lost from the edges during the cutting operation. Section 710 thus lacks a small fruit *sf;* but with this exception, all the features of the longitudinal sections may be traced to and verified in the basal section, bearing in mind that because of varying obliquity and perspective arising from the orientation, from saw-cuts, and from polishing, the actual proportions of parts may appear to fall short of entire correspondence in the drawings. In section 710 a large peduncle and one lesser fruit are rather obliquely cut. Section 709 cuts a large fruit *S* borne by the peduncle so marked on the base-line of Figure 31, and also a large more apical peduncle. Here again there is some

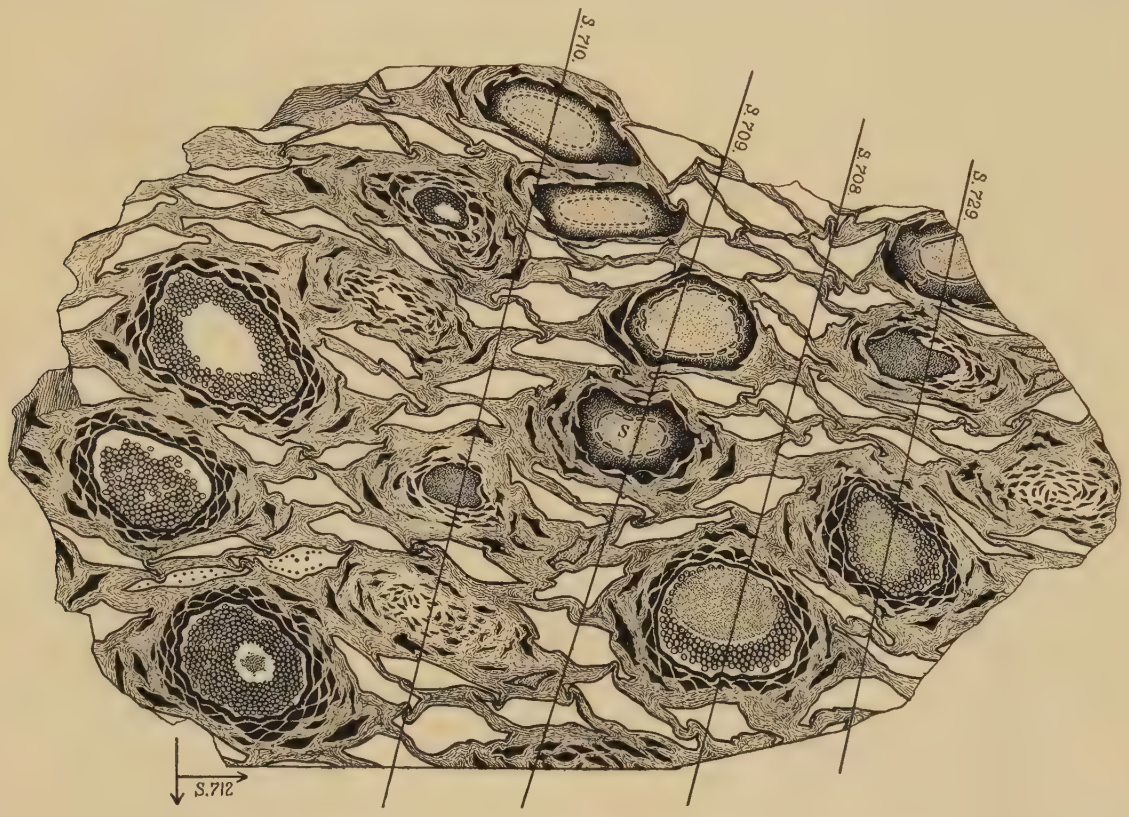


FIG. 31.—*Cycadeoidea Wielandi*, type. Yale specimen No. 393. Drawing of large polished transverse section through armor, complementary to the preceding figure and along with it illustrating the growth stage of all fruits over a large area from the mid-region of the trunk. Natural size.

lateral loss from grinding. Section 708 cuts only leaf bases and one large fruit in the nearly true median plane. Observe the small remaining portion of the parenchymatous cushion and compare carefully with the correspondent transverse section (Fig. 31). Section 729 traverses the peduncle of a large fruit obliquely, then a small ovulate fruit of interesting form, and finally a large fruit in the nearly true median plane.

On turning to the transverse section, Figure 31, one readily observes that the lower side of the cut traverses the armor at a relatively higher level than does the upper side. Seed stems appear in the fruits of the lower side, while on the upper side only the peduncles of four such fruits are cut. Taking the entire section, 10 large and full-grown ovulate cones are found present, with 7 small and immature ovulate cones interspersed between these. Whether by accident or not, both the larger and lesser cones tend to distribution in several

irregularly spiral belts. A little careful inspection shows this fact, especially if it be noted that the longitudinal section No. 712, cut on the base-line as indicated, traverses the young fruit shown in Figure 32. Of the young fruits, only the uppermost one, seen to the left of section 710, has seed stems which have noticeably elongated. This fruit is also shown on Figure 32 (section 742). It may be regarded as a somewhat anomalous member of the larger ovulate fruit series which has failed to grow, or as a young isolated fruit of a following season. It bears an immature disk. All the other small fruits have a rather heavy disk shoulder, from which a functional disk may have dehisced, leaving the ovulate zone to abort. There are, of course, several alternative explanations other than that of monœcism as above suggested.

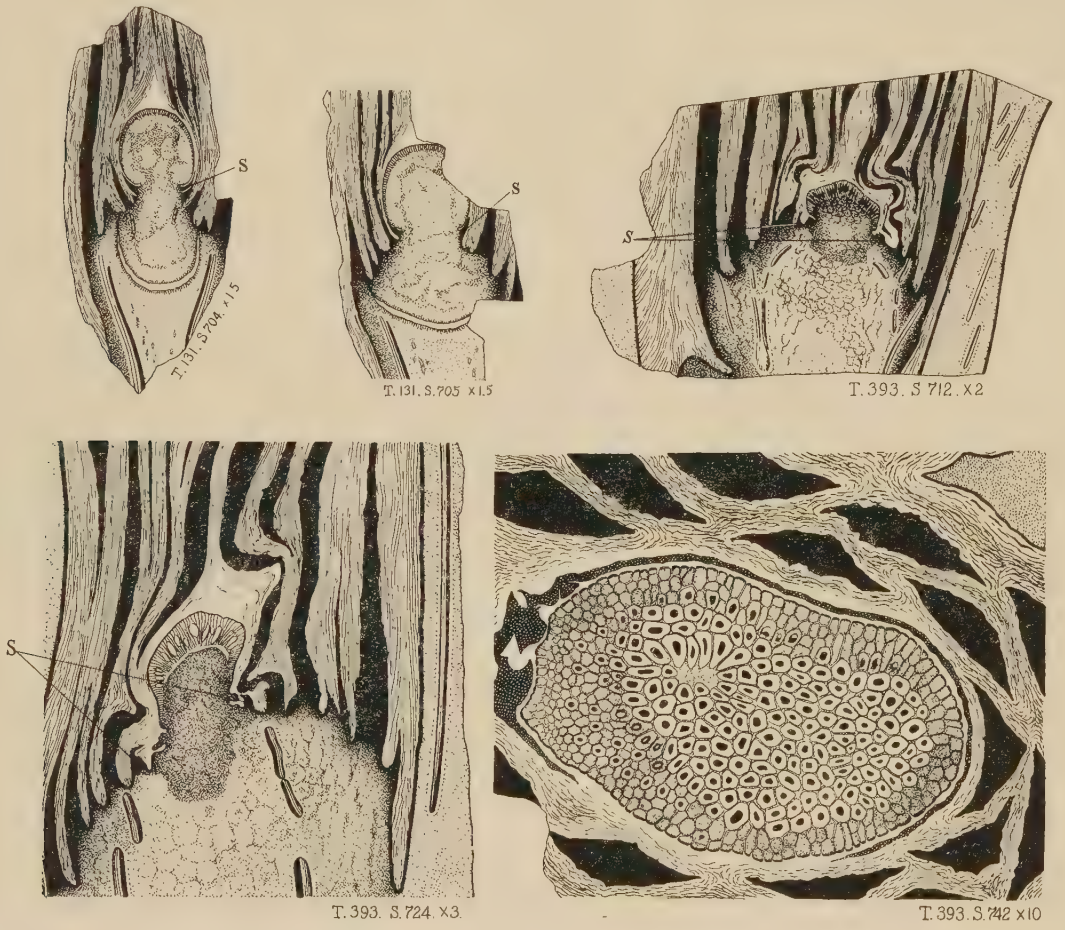


FIG. 32.—*Cycadeoidea Wielandi*, type. Yale specimen No. 393. (With two sections from Yale trunk No. 131.) A figure comparison suggesting two monœcious species. Figures enlarged as marked.

Characteristic longitudinal sections through young fruits, such as are usually borne by the series of lesser peduncles appearing in the large armor section, are shown in Figure 32. There a comparison is also made (sections 704, 705) with Yale trunk No. 131, in which such young ovulate fruits are distinctly more symmetrical than in trunk 393. The sections 712 and 724 are from the latter trunk and exhibit the diminutive ovulate zone and relatively large size of the peduncles, with the prominent disk shoulder (S). In particular it may be noted that section 712 falls below the plane of the fruits of the longitudinal sections of Figure 31. The exact position in the armor is indicated by number in Figure 31.

The transverse section of the young seed-stem zone, section No. 742 of Figure 32, has a unique interest. Conservation is limited to the larger features, which are, however, diagrammatically clear. The dark outer zone of sterile scales has occasional fertile stems interspersed and the whole number of scales and seed stems is fully as great as that of the larger fruits. It is decidedly interesting to find an undeveloped disk inclosing this fruit. Inasmuch as disk remnants are not present in the other small fruits with still smaller ovulate zones, this fruit may be somewhat abnormal. Possibly it failed to produce a functional disk, and its ovulate zone then grew forward for a time, but finally fell far short of reaching a mature size. Or again, three seasons of fruit growth may be indicated—first the numerous ovulate series about to ripen its seeds, second a scattering series in the stage of the fruit of section 742, and third a fairly numerous series in the stage seen in sections 712 and 724.

Whosoever would solve for himself the problem of whether the Yale trunks 77, 393, and 131 are monœcious or not, will examine Figures 32 and 33 attentively. The specimens represent two distinct species, and the more plausible explanation is that in both these species alike the small ovulate cones belong to an aborted series. If so, these axes earlier, or even in a previous season, produced staminate disks complementing the accompanying full-grown ovulate series about equally numerous.

But the excellent conservation of the peduncle bundle cylinder in the lesser floral series, and even of small tracheid strands leading out to the hypogynous disk remnants, scarcely helps us to adjudge at once the question of growth. The bundle cylinders (*cf.* Plate 20, phot. 4), of course, have but a small and thin wood zone as compared with that of the mature ovulate cones, although their tracheids are of much the same appearance. In fact, competent morphologists to whom I have shown these peduncle sections agree with me that one can not readily tell from the structural development alone whether growth had been completed or not when the events leading up to fossilization began.

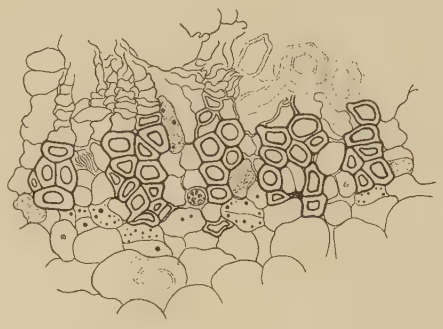


FIG. 33.—*Cycadeoidea Wielandi.* Yale trunk 393. Section 709. × 140.

A xylem sector of the peduncular cylinder characteristic of the small ovulate axes of the preceding figure. Phloem not shown. (Section 709 is from the same peduncle as longitudinal section 712. The base line of the latter marks the level of section 709.

In the camera-lucida drawing, figure 33, it is fairly evident from the development of the xylem, which falls far short of that seen in the cylinder of mature cones (*cf.* Vol. I, text-figures 39 A–C), that growth may be arrested rather than still proceeding. The tangential outer wall of the outermost tracheids of the groups is often thin. Exterior to the field shown there is a larger region of aligned parenchyma and other cells of the phloem. Isolated protoxylem groups like those next the trunk cylinder also occur. Many sphenocrysts traverse the tissues.

Perhaps some later painstaking study of the longitudinal sections of the best-conserved woody cylinders of these lesser flowers, with comparison of the peduncle cylinders of the older cones, aided also by any such factors of control as may be derived from comparisons of the staminate supply in *Tumboa* or of conifer axes of limited growth, may yield a more conclusive answer. It does seem, however, as above concluded, that the general appearance of the smaller flowers, especially the somewhat irregular contours of the ovulate cones, suggests that they were abortive, and is the main evidence on which the case must rest until the discovery of further trunks with their flowers conserved in other stages of growth than

those described. Such might clearly show the time at which the disk first appears, and also the comparative rate of disk and ovulate growth. In any case the large sections on which these additional notes are based, showing the actual condition over a characteristic armor area, demonstrate once more the value of quantitative versus qualitative studies of fruiting conditions in Cycadeoidean trunks.

A symposium of wood zone, cortex, armor, and fruit sections from the Yale trunks 77 and 393 is illustrated on Plates 31 and 32. Reference to those photographs will, in conjunction with the foregoing figures, afford as complete a picture of stem and fruit anatomy as might fairly be expected. As already pointed out the principal features yet requiring closer study are the distribution of wood parenchyma and the exacter course and origin of the peduncular bundle strands which unite to form the cylinder, together with the degree of union with the axillary leaf trace. But the essential facts are already visible. The manner in which the leaf traces rise directly from the lower angle of the meshes of the woody cylinder and form a broadening leaf gap as they pass out through the thick cortex is particularly clear in Plate 31, photographs 4–6. There, too, one notes the even strength of the leaf traces throughout their cortical course; likewise the fact that lesser peduncle strands only begin to appear in the outer cortex, but then unite as right and left strands to form the bipartite axillary trace a little before the trough-shaped leaf trace first begins to split into the bundles later subdividing into the series forming the regular leaf-base pattern. Furthermore, a section of large area like that shown on Plate 32, photograph 2, is virtually a serial section so far as any single traces are concerned. It is clear enough, therefore, that the peduncular bundle cylinders have but little direct connection with the main trunk cylinder. The same condition will later be noted in *Cycadeoidea Dartoni* with a similarly thick cortex. The origin of the peduncle strands has not been studied in the case of any of the trunks with a thin cortex. But in such the condition must doubtless approximate that of axillary shoots in ordinary stems lacking abnormal cortical development.

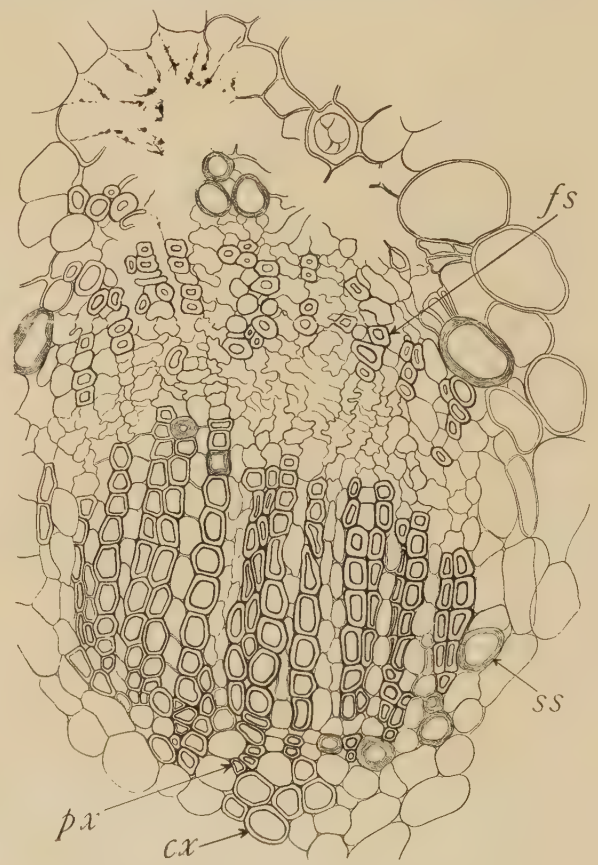


FIG. 34.—*Cycadeoidea Wielandi.* Yale trunk 393, section 709. ×140.

Leaf-base bundle development in the mid-armor. *cx*, centripetal xylem group of 6 large cells; *px*, protoxylem followed by main body of centrifugal xylem; *ss*, sheath sclerenchyma, which is far less extensive than in most species; *fs*, fibrous sclerenchyma of the outer phloem region

The features of the leaf-base bundles, Figure 34, are characteristic for the species and afford an interesting comparison with the much more lignified bundles of *C. colossalis*. Similar contrasts are afforded by various unfigured species. (*Cf.* Fig. 27, and Vol. I, Plate XX.)

Cycadeoidea Paynei[1] Ward, 1898.

1898. WARD. Proc. U. S. Nat. Mus., Vol. XXI, p. 213.
1899. WARD. Pt. II, Ann. Rep. U. S. Geol. Surv., XIX, pp. 620–621, Pls. CXIII, CXV.
1900. WARD. Am. Jour. Sci., Vol. X, p. 333.
1906. WIELAND. American Fossil Cycads, Vol. I, pp. 130–131, 163–164, 167, 115, 116.

As the result of as yet very incomplete histologic study of the U. S. National Museum type No. 5, illustrated in the subjoined figure 35, it has been found that the conservation is of marvelous beauty and perfection, while the wood structure somewhat differs from that observed in any other sections cut from either American or European cycads, because of

FIG. 35.—*Cycadeoidea Paynei.* Slightly reduced view of polished median section through base of U. S. National Museum type trunk No. 5.

The medulla 7 cm. in diameter, xylem 1 cm. in thickness, the distinct cambium marked by the three arrows, the phloem 5 mm. in thickness, the cortical parenchyma 5 to 8 mm. in thickness, and the exterior armor of old leaf bases about 1.5 cm. thick, all appear with diagrammatic clearness in this illustration, which also gives a very clear idea of the manner in which silicification ceases at the base of the Cycadeoid trunks without root conservation.

an unusually freely pitted appearance of the medullary ray-cells. True enough, this character, which is unknown in existent cycads and is developed in a slighter degree in some of the Cretaceous conifers, is also found in *Bennettites Gibsonianus* and other forms; but in no case are the ray cells quite so characteristic as in the National Museum type. As a consequence of this unusual conservation and interest, there has been begun, through the courtesy of Dr. Knowlton of the National Museum, a systematic study of a trunk wedge, the results of which must be brought out at some future time. Obviously when a study of

[1]It would be very desirable to correct the spelling of this name, which is rightly *Paine.* The best usage must permit such corrections, certainly where the direct testimony of those familiar with all those concerned may be had. The name *Cycadeoidea Macbridei* is similarly misspelled in places, the spelling *McBridei* depending on a mere typographical error.

a perfectly conserved trunk wedge has been completed and the character of the cylinder from base to apex is once fairly illustrated, *Cycadeoidea Paynei* must take rank as one of the most interesting species of Cycadeoids known, despite the fact that thus far no fruits have been found. The meaning of the branch-like appendage on the left side of the fine median longitudinal trunk section figured by Professor Ward on his Plate CXV has not yet been determined. Some young fruits may very well be present in the distinctly heavier armor of the upper half of the trunk from which larger sections remain to be cut.

Other sections of much interest must yet be cut through the cortex, showing the leaf-trace spirals, which must be quite striking, owing to the small size of the old leaf-bases.

In order to illustrate not merely the present status of *Cycadeoidea Paynei*, but that of most American fossil cycads and all foreign species where the type is not based on and confined to a single specimen, Professor Ward's original description is here given in full:

"*Cycadeoidea Paynei*, n. sp. (Pl. CXIII–CXV).—Trunks medium-sized, laterally compressed, usually enlarging from the base upward to near the summit but sometimes subcylindrical, 30 to 55 cm. high, 65 to 85 cm. in average girth, 20 by 25 cm. to 25 by 35 cm. in diameter, light or darkish brown in color, not specially firm or heavy, bearing few or not any secondary axes; organs of the armor horizontal; phyllotaxy rather obscure, but scars arranged in imperfect spiral rows, chiefly subrhombic, but varying to rhombic or triangular, much distorted in the specimens in hand, but where clearly shown 10 to 16 mm. high and 16 to 31 mm. wide, empty to some depth, their bottoms filled with the partially decayed remains of the petioles; ramentaceous interstices rather thin but variable, usually with a more or less distinct commissure; reproductive organs or their remains numerous and conspicuous, often projecting considerably beyond the general surface in the form of protuberances or terete spongy cylinders, often decayed, leaving large cavities more or less crater-shaped or funnel-shaped, the interior sometimes definitely grooved or marked, surrounded by numerous, sometimes large, triangular involucral bract scars; armor varying in thickness from 2 to 7 cm., attached by an irregular line or thin layer of bark to the cortical parenchyma which is 1 to 2 cm. thick and incloses a fibrous cone of about the same thickness, which is divided into two or three rings; medulla less compressed than the outer parts, 6 to 10 cm. in diameter.

"The only specimens that certainly belong to this species are Nos. 4 and 5 of the collection purchased from Mr. Cole. The description of the internal parts is chiefly based on No. 5, which is the smallest of that collection and has been cut longitudinally through the axis, one of the halves cut transversely 12 cm. above the base and the surfaces polished. These sections furnish clear views of the organs of the armor and of the relations of the armor to the underlying parts. The specific identity of the two specimens is based on the external characters, which substantially agree. No. 4 weighs 33.11 kilograms and No. 5, 22.22 kilograms. I name the species for the ranchman, Mr. Payne, who originally discovered the cycads of that region and from whom Mr. Cole obtained them. He it was, moreover, who finally guided us to the locality after Mr. Cole had vainly sought to take us to it the previous day, missing the way notwithstanding that he had been at the spot.

"In the Yale collection there are two specimens, Nos. 58 and 69, which I have doubtfully referred to this species, although some of the characters are different from those above described. They are vertically instead of laterally compressed. If this is due entirely to pressure of the superincumbent mass after entombment, it has no systematic value and depends upon the position occupied by the specimen; but eminent authorities have insisted that it is a condition of growth. I am inclined to think that this may be true in some cases, but that the former explanation is the chief one.

"The Yale specimens are both smaller than either of the National Museum types, No. 69 weighing 20.86 kilograms, and No. 58, which is dwarf, abnormal, and perhaps immature, 5.33 kilograms.

"Pls. CXIII and CXIV give side and base views of the type specimens Nos. 4 and 5 of the U. S. National Museum, and Pl. CXV represents the polished surface of the interior of No. 5, bringing out the relations of the various tissues in a very satisfactory manner.

"All the specimens are from the Minnekahta region."

Subsequently to the publication of the foregoing description, Professor Ward, in the winter of 1900, following a great accession of material brought to the Yale Collections

through the activities of Professor Marsh and others, including the writer, ascribed to *Cycadeoidea Paynei* various additional Yale Museum specimens numbered as follows:

52?, 132, 165, 263?, 293??, 334, 364, 395?, 423?, 448, 452, 713.
58?, 135, 188?, 272, 316, 336?, 376, 399, 428?, 451?, 493?,
69?, 163?, 247?, 280?, 319??, 337?, 386, 413?, 434?, 557, 712,

As already stated, the section-making from the Yale Museum specimens has not definitely confirmed the accuracy of ascription to *C. Paynei* in the few instances taken up, and all reference of material to *C. Paynei* in Volume I is subject to doubt and revision. In most instances the trunks are probably referable to *C. Wielandi*, it being certain that the arbitrary aggregate of specimens called *C. Paynei* includes two if not three or four distinct forms; similarly, some trunks of *C. Paynei* are doubtless hidden among the long list of specimens called by other names, although it seems quite certain that whatever the changes resulting from future study, *Cycadeoidea Paynei* will not be found a prolific species. Therefore, as the case of *C. Paynei* stands to-day, this species is founded on a single very incompletely studied type, the U. S. National Museum No. 5, and the reference to it of other specimens is in all cases very uncertain or positively in error. The wood of the basal segment is illustrated on Plates 30, photograph 1; 33, photograph 4; 34, photographs 3, 4; 35, photographs 3, 5, and 36, photographs 4, 5.

Cycadeoidea protea (Ward).

1900. Am. Jour. Sci., 4th ser., Vol. X, pp. 343–345, and Pl. IV, No. 457.

The heterogeneous assemblage of trunks brought together by Professor Ward under the suggestive name *Cycadeoidea protea* has a certain biologic significance in any continuation of fossil cycad study, despite the fact that no sections have as yet been made which finally prove the presence of any such additional small and branching species among the Minnekahta trunks. But in giving a further notice of this "species" there is no need to either repeat the initial description or redescribe any of the trunks. In fact, it would have answered ordinary requirements if in the original description it had been explained merely that after dealing with the larger species from Minnekahta, and setting aside those lesser trunks which might be referred to the small branching *Cycadeoidea nana*, there still remained a dozen or more much-branched and even gnarled specimens a kilogram or two in weight, with very small leaf bases and occasional traces of small buds, either vegetative or fruit, which could not be outrightly declared juvenile, and which might well be specifically distinct. The trunks and branches referred to *C. protea* are the smallest Cycadeoideans known, and embrace 20 Yale specimens, with one in the National Museum, as follows:

No.	Weight.	Condition.	No.	Weight.	Condition.
*19	1.81 kg.	Nearly complete.	382	1.25 kg.	Nearly complete.
32	2.61	Complete.	414	3.52	Nearly complete.
185	0.94	Nearly complete.	457	1.47	Complete.
187	0.14	Nearly complete.	458	1.47	Incomplete.
241	1.59	Nearly complete.	463	0.56	Fragment.
253	1.02	Fragment.	466	0.68	Incomplete.
296	1.25	Nearly complete.	487	3.18	Nearly complete.
297	0.34	Fragment.	499	0.68	Nearly complete.
303	1.59	Nearly complete.	521	0.79	Nearly complete.
315	0.91	Nearly complete.	529	0.22	Nearly complete.
359	1.81	Nearly complete.			

*U. S. Nat. Mus. specimen.

Although it seems probable that some or most of these gnarled, fragmentary, often much chalcedonized, and for the greater part rather indifferently silicified specimens are merely young forms of various larger species, or even include examples of *Cycadeoidea mirabilis*, such a fact is difficultly determinable. It is only conservative to note the likelihood that one or several small and distinct species are really included among these inconspicuous members of the great assemblage of branching trunks from Minnekahta. Furthermore, the species *C. protea*, even though considered as one of convenience, serves well to emphasize the fact that any departure from the normal *Cycadeoidea* structure is most likely to occur among just such small and rather obscure specimens. Such trunks also suggest the microphyllous members of the closely related Williamsonian tribe, especially characteristic of the Liassic. Vegetatively, these differed mainly from *Cycadeoidea* in their still more pronounced branching habit with a rather free development of long scale-bearing internodes. It is easy to see, therefore, that sooner or later forms having some or all of these characters are likely to be found in just such assemblages of Cycadeoidean trunks, and that any such would have much the aspect of the trunks called *C. protea*. Considerations such as these do give to the series of trunks in question a certain interest and importance.

It is very probable that the well-represented species *C. minima* described at the same time as *C. protea* (*loc. cit.*, pp. 341–343) is a synonym of the latter. But following the method pursued throughout this work no pronouncement is made on this point in the absence of a series of sections. None is necessary. In handling this series of specimens, which holds much interest for the same reasons just given in noting *C. protea*, no superficial characters of special significance were noted. The specimens are recorded as follows, the first 15 being in the Yale Museum:

No.	Weight.	Condition.	No.	Weight.	Condition.
53	1.57 kg.	Complete.	157	0.23 kg.	Nearly complete.
149	1.22	Complete.	168	2.15	Complete.
150	1.39	Complete.	426	0.30	Fragment.
152	0.79	Complete.	468	0.45	Nearly complete.
153	0.45	Complete.	474	0.45	Incomplete.
154	0.45	Complete.	478	0.11	Fragment.
155	0.34	Complete.	714	1.36	Complete.
156	0.30	Complete.	*2248	0.62	Nearly complete.

*U. S. Nat. Mus. specimen.

It is certain that for these many forms some better designation than "*indeterminable*" is desirable, and because branching is a frequent character the name *protea* may well be given the preference for these small trunks of uncertain specific attribution.

Cycadeoidea excelsa Ward.

1898. WARD. Proc. U. S. Nat. Mus., Vol. XXI, pp. 225–227.
1899. WARD. Ann. Rep. U. S. Geol. Surv., XIX, pp. 637–639, Pls. CLIII–CLV.
1906. WIELAND. American Fossil Cycads, Vol. I.

The type of the present species is somewhat arbitrarily included within the Minnekahta group. Although found weathered out in a ravine, as Professor Ward relates (p. 638), 15 miles eastward of the main Minnekahta locality, there is no especial need to separate this isolated specimen from the Minnekahta group, for scattering Cycadeoids have been found along the intervening "rim" slopes and the topography does not noticeably change.

In fact, the Minnekahta series is best considered as indicating a great Cycadeoid forest with outliers circling around the southern Black Hills edge in the form of a long, shallow crescent with horns at least 20 miles apart. Figure 8*a* shows the "Rim" near the *C. excelsa* locality.

From any point of view the type specimen of *Cycadeoidea excelsa* must be regarded as one of the most interesting of all Black Hills trunks and, as pointed out in Volume I, it is the American counterpart of *Cycadeoidea gigantea* of the Isle of Portland, the tallest of all European trunks.

As originally described and photographed, *C. excelsa* type is composed of four joined segments with a total altitude of 91 cm., both base and summit failing of recovery. But in the autumn of 1900, at the same time that I secured for the American Museum of Natural History the collection mentioned in Volume I (p. 8, footnote), I found that the local Minnekahta mineral dealer still retained a fifth segment of the type *C. excelsa* basal to the others, but likewise incomplete. This segment, of irregular shape and a height of about 25 cm., I bought along with the collection sent to the American Museum, arranging to have it sent directly to the National Museum. Unfortunately I have until recently remained under the misapprehension that this type segment was duly forwarded and received. But I now find no record of its receipt and fear that it has been lost to science through my neglect to keep it in my own hands instead of trusting its shipment to others.

Very recently the apical fourth segment of the type as figured by Ward has been sawed through longitudinally and one of the surfaces has been polished. In this polished longitudinal trunk section all the structure zones are diagrammatically clear and it is of much interest to find the wood zone retaining full size and diameter without noticeable variation in thickness. Nor is there, so far as may be made out from superficial examination, any markedly increased thickness in the wood zone of the basal segment. In fact, the re-examination of the type reveals no tapering at either base or summit, and it now seems clear that from 1.3 to 1.5 meters must be taken as the minimum height of this interesting columnar type. As bearing on both height and wood-zone development, it of course remains desirable to supplement the apical longitudinal section with the corresponding section of the basal segment.

Somewhat extended mention of *C. excelsa* has already been made in connection with the description of *Cycadeoidea Jenneyana*, and inasmuch as a more persistent study of the histology of these species is still to be carried out, it is preferable to leave the earlier notes unchanged; but now that a good longitudinal section of the apical trunk segment is available, it is of interest to compare the dimensions with those of the more basal transverse trunk section of *C. Jenneyana* (photographed on Plate 8) as follows:

	Diameter.	Medulla.	Wood (×2).	Cortex (×2).	Armor (×2).
Cycadeoidea Jenneyana (Y. T. 102).....	48−	17+	3	4	20+
Cycadeoidea excelsa type.....	32	13.5	4	4	9+

Inasmuch as it is certain that the section of trunk 102 traverses the lower half of the stem, while the *C. excelsa* measurement is from far toward the summit, these dimensions alone conclusively indicate two distinct species; for while as compared with *C. Jenneyana* the type *C. excelsa* is the more slender and has rather the smaller leaf bases, the wood zone (even when measured at so much the higher level) is not only relatively to diameter but in actuality the heavier. The *C. excelsa* armor, owing to the long period of weathering to which the stem must have been exposed while being eroded out of and transported from

its original position, is much broken away, although in places reaching a depth of 7 to 8 cm., or about the same proportional development as in *C. Jenneyana.*

Measurements of zone dimensions of existing cycad trunks show, it is true, certain marked variations. Thus, in a small group of *Zamia floridana* trunks a very marked zonal variability was observed, as follows:

Zamia floridana.	Length.	Diameter.	Medulla.	Wood.	Cortex.
Unbranched trunk (full grown).....	15	6	1.5	.2	2.2
Base of a forked trunk.....	10	9	3	.3	3
Another forked trunk.....	10	9	2.7	.25	3
A cone-bearing branch.....	..	6	1.5	.2	2
Another branch.....	..	6.5	1.6	.3	2.3
Another cylindrical stem.....	15	5.7	1.6	.3	1.7

Doubtless a more extended and more fully representative series would exhibit even greater disparities. Nevertheless, these variations in *Zamia* trunks are more suggestive of the caution required in studying the sections of branched than of columnar Cycadeoideas. In fact, it seems reasonable to expect that the norm can be readily established in the case of the strictly columnar forms. They must conform much more nearly to the given type, and it is to be hoped that longitudinal sections or their equivalent in transverse trunk sections at known heights may in the course of time be cut from trunks sufficiently complete to yield the critical data. While we may expect in the group every variation from an enormous pith and cortex to a preponderant wood development like that of dicotyls or conifers, the appearance of the woody cylinder in forms like *Cycadeoidea Dartoni, C. etrusca,* and the present and various other types strongly suggests a marked uniformity in the entire stem anatomy for a given species.

With regard to fructification; on careful search over the outermost armor portions yet remaining a few young ovulate fruits were observed. These, owing to the granulation due to weathering, do not retain well-marked structure, at least in their outer portions and (like the wood) as yet lack the needed thorough study in thin section; but on breaking away the terminal portion of one of the fruits it was found to have the most elongate type of convex or rounded cushion yet observed. In fact, the cushion may even reach an elliptical form and thus constitute the final link in the series passing from the flatly convex to the elongate conical cushion.

GENERAL STATUS OF MINNEKAHTA SPECIES.

In the foregoing annotation of species, attention has been mainly confined to the more or less certainly established and more or less reasonably defensible specific groups discernible in the great series of Cycadeoidean trunks from the Minnekahta sector of the Black Hills Rim. This unapproachably magnificent series of silicified trunks, mainly and uniquely composed of gigantic branched forms, with a few lesser or pygmic species, now numbers upwards of 600 specimens—probably more splendidly conserved forms being included than have ever been recovered from the localities of all the world besides. These specimens are mainly included in the Yale collections where upwards of 500 are conserved. A small and fine group, including the huge type of *Cycadeoidea colossalis* and the imperfect but splendid branched specimen arbitrarily called *C. minnekahtensis,* forms the most important part of the rich Cycadeoid collections of the United States National Museum. A still finer series is that of the State University of Iowa, illustrated on Plate 13. Four of the finest trunks are in the British Museum at South Kensington, where they were early sent by Professor

Macbride as a compliment to William Carruthers. But as the early collections were rapidly followed by a series of examinations of the Minnekahta locality, resulting in the Yale collection, and as these were made thorough so far as superficial collection could go, relatively few Minnekahta specimens have found their way into isolated collections.

A few trunks from Minnekahta have been acquired by the Geological Department of the University of Nebraska; a few other trunks are in private hands, where they are, of course, more or less lost to view and always in danger of final loss.

As annotated in the foregoing pages, the valid Minnekahta species include the great bulk of the collections and are some 9 or 10 in number, simply characterized as follows:

(1) *Cycadeoidea dacotensis*, a huge, much-branched type bearing the largest fructifications known. The microsporous disk is composed of 17 or 18 fronds.
(2) *Cycadeoidea Marshiana*, likewise a strikingly branched form, but with a lesser staminate disk of only 11 or 12 component fronds. [This formula is in any case correct, and the validity of the species does not depend on the primary type alone. Reexamination of sections shows that this may also prove to agree with the secondary types.]
(3) *Cycadeoidea Macbridei*, a species of very unsatisfactory status, the synonymy of which remains to determine.
(4) *Cycadeoidea colossalis*, a huge type apparently characterized by small leaf bases, large bracts, and medium-sized fruits as yet unstudied.
(5) *Cycadeoidea nana*, the smallest of the branching forms, and separated from all of the branched types by its ovulate cone, which is of the short, convex cushion type, instead of elongate.
(6) *Cycadeoidea Wielandi*, a medium-sized form somewhat more columnar than the foregoing, characterized by a fine series of ovulate cones. This species may or may not prove finally valid, although in its present status it is, with the single exception of the still more striking Hermosa type *Cycadeoidea Dartoni*, the best-studied Black Hills form. This is, of course, mainly due to the convenient size for sectioning of Yale trunks 77 and 393, combined with remarkable conservation.
(7) *Cycadeoidea Paynei*, separated from the foregoing species by its smaller leaf bases and freely marked medullary-ray cells, study of the type being as yet incomplete, and mainly confined to the woody cylinder. The type is young and remarkably well conserved, but with few or no fruits.
(8) *Cycadeoidea protea*, an arbitrary heterogeneous assemblage of unstudied specimens, in all probability mostly juvenile, but probably including a true microphyllous type.
(9) *Cycadeoidea excelsa*, a distinctly columnar stem like the Isle of Portland *C. gigantea*, certainly distinct from any of the foregoing species and analogous to Black Hawk forms like *C. Jenneyana*.

In segregating the foregoing 9 possible species regard has been had for *priority*, *structure* as far as possible, and, frankly speaking, *probability*. It would at the present time be as unreasonable and illogical to expect final accuracy in diagnosing even these species as to maintain that it has been reached. It has, however, been consistently and persistently held that it is worth while to establish the species in the fullest degree of finality, and unquestionably the best method of study must henceforth be to take up important types and study them thoroughly one by one on the basis of adequate trunk sections and thin sections.

Unfortunately a residuum of doubt as to the exact status of the primary Minnekahta type *Cycadeoidea dacotensis* Macbride and the relation to it of the two secondary species *C. minnekahtensis* Ward and *C. superba* Ward remains uncleared, although if these latter species are exactly synonymous with *C. dacotensis*, as seems quite possible, the main species tangle can soon be gotten rid of. It is regrettable that with all the wealth of material in this country and the number of able investigators available, *Cycadeoidea dacotensis* type remains unstudied. There is no valid scientific reason for this failure. This type is not a huge or difficult specimen to handle, like either *Cycadeoidea ingens*, *C. Reichenbachiana*, or *C. colossalis*. Sentiment should play no part here and the author feels in duty bound to state that he offered to carry out the sectioning of this type with the greatest precision possible, and to give such work wholly without cost to the conservators. But objections were raised, just as they were raised by the curators of the Zwinger Museum some thirty years ago when Count Solms-Laubach offered to section *Cycadeoidea Reichenbachiana* (*q. v.*) A subsidiary study of the Yale trunk No. 54 (*cf.* Vol. I, Plate V, photograph 2) is now being

carried out. The larger sections have already been cut, along with various others, at the United States National Museum through the courtesy of its officials. The series also includes a polished longitudinal section of the Isle of Portland *Cycadeoidea microphylla*, trunk No. 801 of the Yale collections, shown on Plate 3, photograph 5. These important trunk sections afford comparative measurements of too much interest to omit:

The Yale trunk No. 54 bears, allowing for a few incipient branches, an even 50 axes of fructification. A few of the axes near the base are ovulate cones of large but not mature size, the seeds being small. The largest of these immature cones reaches 5 cm. in diameter. The form is that of a pear, in a way repeating the outlines of the trunk itself. The larger and basal fruits may be even a full season in advance of the 40 axes of the mid and upper trunk region, where fruiting is least advanced. Two seasons of fructification, one basal and scattering, the other culminant, appear probable. The main season of fruit growth was marked by the production of fruits all over the middle and upper region of the trunk, with gradual decrease in size toward the apex. This was essentially the condition found in Yale cycad 214, made the subject of extended study in Volume I. In that specimen, however, there are fewer ovulate cones of large size near the base, and at least 3 of the axes of the mid-region still bear staminate disks; no cones or disks are developed in the axes grouped around the crown, although the peduncles are of full size. The conclusion reached in the case of Trunk 214 was that a few scattering basal fruits were followed by a main season of bisporangiate fruit growth followed by scattering apical fruits in part possibly more or less abortive. Trunk No. 54 appears to agree. Although it bears the larger basal cones these are yet quite young, and it is possible that the main fruit series has not developed its disks. There may be a certain tendency to continuous fruit production, beginning at the base. The terminal bud has the appearance of being made up of scale leaves as in the type of *C. Dartoni.*

The Isle of Portland trunk 801 is slightly younger; no large basal cones appear in the longitudinal section, but one may see 3 very young lateral cones deeply embedded in ramentum. The conical form is deceptive, being due to vertical crushing combined with a less extensive conservation of the upper armor. There are doubtless more scale leaves towards the truncated apex; but the section indicates a more columnar form than Yale trunk No. 54, which is comparable in size. The trunk was probably fossilized in the position in which it grew. The woody cylinder was much macerated below and is in places broken up and floated out of position, so that accurate basal measurements can not be had; but from a distance of 20 cm. up, the wood conservation is quite equal to that usually found in Black Hills trunks. The armor is at no point either distorted or much crushed out of position, and the 3 small and young fruit axes noted in the longitudinal section of the entire trunk compare interestingly with the 5 somewhat more advanced axes visible in the field of the longitudinal section of trunk 54. It is not probable, therefore, that the woody cylinder would have undergone much subsequent growth or a later increase in thickness. The same is true of the columnar type *Cycadeoidea Paynei* of the United States National Museum, a further comparable form with small leaf bases, and still in its *pulcherrima stage* (defined, Vol. I, p. 186). The foregoing data for age and development being so complete, the comparative measurements afforded by these trunks have unusual interest. The maximum dimensions of the principal trunk regions of all three are ranged in the order of departure from the globular type as follows:

Trunk dimensions.	C. dacotensis (?) (Yale trunk No. 54.)	C. microphylla. (Yale trunk No. 801.)	C. Paynei (type). (U. S. Nat. Mus.)
	cm.	*cm.*	*cm.*
Height	44.0	48.0	30.0
Diameter, total	39.0	38.0	21.0
Armor, thickness	10.0	10.0	3.0—
Medulla, diameter	12.0	12.0	8.0
Woody cylinder, thickness	1.5+	1.0+	1.5
Xylem	1.1	0.7	1.0
Phloem	0.4	0.3	0.5
Cortex	3.0	1.0	2.0
Terminal bud, length	8.5	....	5.0

The agreement here brought out sets at variance any contention that these forms can not be included within one and the same genus. Observe that in the Isle of Portland *C. microphylla* the woody cylinder is measured 28 cm. beneath the incomplete summit. Judging from the other two trunks the increase in thickness of the wood zone at the base could not possibly have exceeded 1 cm. It therefore appears that the woody cylinder is monoxylic and not as massive as in *Cycadeoidea megalophylla*. The monoxylic feature was not determinable from the exterior appearance. In fact at the base there is a sort of radiation in the medullar tissues simulating or suggesting wood structures. Something similar may be observed in the fine trunk from Minnekahta shown on plate 26 where conservation extends near to the zone of root insertion. None of the Portland specimens with conserved armor appear to be polyxylic.

SPECIES OF UNCERTAIN STATUS.

Finally, it remains to mention very briefly the Minnekahta specimens of wholly uncertain status arbitrarily described as *Cycadeoidea Colei, C. furcata, C. insolita, C. minima, C. occidentalis, C. pulcherrima, C. turrita, C. Wellsii, C. superba,* and a closely related form from the northern Black Hills found in the Inyan Kara mountain or Sundance region, *C. heliochorea*. These may all be justly classed as species of undetermined status, most of which, if not all, will prove to be synonyms of precedent forms.

The 10 Minnekahta species of wholly doubtful validity just mentioned may be somewhat succinctly dealt with. *Cycadeoidea Colei*, which is a handsome "type" of the United States National Museum series, is probably a *C. Marshiana*. The remainder are Yale specimens. The *C. furcata* (*cf.* Plate 22) is also adjudged to be a *C. Marshiana; C. insolita* may fall in the *C. Wielandi* or *C. Paynei* group; *C. minima* may be either juvenile or a true microphyllous form; *C. turrita* may be included in *C. Wielandi* or *C. Paynei;* and *C. occidentalis* has no status except as a possible *C. superba*, itself little known. *C. pulcherrima*, as explained in Volume I, is only a growth stage of *C. dacotensis, Marshiana,* or *colossalis*, the *pulcherrima* stage being the growth interval between trunk maturity and the emergence of the main fruit series, which throws the leaf bases out of their initial symmetrical spiral succession. *C. turrita* is probably *C. Wielandi* or at least a *C. Colei*. *C. Wellsii* type merits further study, but has the general appearance of a *C. dacotensis* with rather smaller flower buds than usual. The study of *C. superba* could more logically follow the sectioning of *C. dacotensis*, and *C. heliochorea* requires no further present mention.

In enumerating these arbitrarily named and mostly redundant species, which at least have a certain kind of catalogue value, it has seemed wholly unnecessary to give page and plate references for the specimens as described and illustrated by Professor Ward in Report 19 of the United States Geological Survey. But inasmuch as these forms may from time to time receive the attention of students, it is well to append the following list of Yale Museum arbitrary types and assignments of specimens:

(*A*) *Cycadeoidea Colei:* Nos. 12, 20, 25?, 28?, 48, 52?, 57, 68, 80?, 224?, 240?, 246?, 291, 321, 433, 444, 476?, 539.
(*B*) *Cycadeoidea furcata:* Nos. 18, 60, 718.
(*C*) *Cycadeoidea insolita:* Nos. 50, 64?.
(*D*) *Cycadeoidea minima:* Nos. 53, 149, 150, 152, 153, 154, 155, 156, 157, 168, 426, 468, 474, 478, 714.
(*E*) *Cycadeoidea occidentalis:* No. 234.
(*F*) *Cycadeoidea pulcherrima:* Nos. 78, 159, 545.
(*G*) *Cycadeoidea turrita:* Nos. 15, 35?, 45, 49, 51, 65, 66, 67, 74, 75, 82, 85, 139, 141, 151?, 166, 183, 190?, 191?, 223?, 255??, 261?, 269, 270?, 278, 295??, 304?, 313, 323, 330, 352?, 360, 368, 374, 394, 402, 406, 408?, 409, 446?, 450?, 482, 483, 484, 486, 519??, 731.
(*H*) *Cycadeoidea Wellsii:* Nos. 21, 59, 130, 136, 138, 222, 243, 322, 391, 400, 500, 501, 537.
(*I*) *Cycadeoidea superba:* Nos. 137, 146, 147, 218, 717.
(*K*) *Cycadeoidea heliochorea:* Nos. 722, 723, 724, 725, 726.

It is of further importance to record the fact that out of consideration for European paleobotanists especially interested in the silicified cycads, the following numbers of the Yale

collection from Minnekahta have been transferred to European Museums. In nearly all cases they represent the finest of trunks; for it was held that the number of trunks which could be subtracted from the greater Yale collection previous to long years of elaborate study must be limited and that the only effective manner in which limitation could be profitably set would be to send abroad nothing but the best and most distinctive material, and then only to those much interested. Lesser specimens have for exhibition purposes no significance comparable to their value for study material or sectioning, and can not be advantageously studied after isolation from the the main collections. Such could only misrepresent the truly magnificent character of the American series. The specimens selected to illustrate the American series in European collections still retain the arbitrary names originally assigned by Professor Ward, as follows:

No. 112. *Cycadeoidea dacotensis.* Weight 70 kg. A nearly complete exceptionally symmetrical trunk terminating in a splendid crown of young leaves clearly showing the ranked pinnules. Bears many well-advanced fruit growths. See text-figure 4. Also segments Nos. 73 and 231, called *C. turrita* and *C. Macbridei.* Naturhistoriska Riksmuseum, Stockholm.

No. 242. *Cycadeoidea minnekahtensis.* Weight 107 kg. A fine central stem with branches and summit broken away. Bears various ovulate cones and younger fruits. See text-figure 3. Also No. 144, a *C. minnekahtensis* summit with young fruits. Botanical Department of the University of Cambridge, England.

Nos. 405, 711. *Cycadeoidea Marshiana.* Weight 25 kg. No. 216, *C. Marshiana.* Weight 60 kg. Bears at least one bisporangiate fruit. No. 63, *C. dacotensis.* Weight 16 kg. Summit of medium-sized trunk. Bears fruits and adventitious, partly emergent frond with ranked pinnules. University College, London.

No. 216. *C. Marshiana.* Weight 58 kg. A good base; terminates as a "crow's nest," but bears one complete branch and fruits in bisporangiate stage; a very handsome specimen. Université de Caen, France.

No. 276. *Cycadeoidea Marshiana.* Weight 150 kg. Three of four symmetrical branches ending in "crows' nests." This is the only instance where a branched trunk consists in four close-set, equally developed branches. The trunk is uniquely interesting. In *pulcherrima* stage; only very small axes of fructification. Jardin des Plantes, Paris.

No. 501. *Cycadeoidea Wellsii.* Weight 157 kg. Although a small portion of the summit is missing, this immense specimen of oval form must rank as one of the finest ever collected at Minnekahta. It is just emerging from the *pulcherrima* stage and bears many young fructifications all over the lateral surface. The structure is in the main well conserved. In quite every respect this specimen vies with and in some points excels the only European specimen comparable to it, the great *Cycadeoidea Reichenbachiana* of the Zwinger Museum. Ecole des Mines, Paris.

No. 138. *Cycadeoidea Wellsii.* Weight 80 kg. A rarely fine and complete exhibition specimen just emergent from the *pulcherrima* stage, with a striking fruit series. Also No. 158. *Cycadeoidea dacotensis.* A remarkably handsome specimen. See illustration by Capellini (reference 46). This trunk was, however, sawed in two at Bologna and half returned to the Yale collection (*cf.* fig. 15). Capellini Museum at Bologna.

CHAPTER VII.

THE HERMOSA CYCADEOID.

The remarkable U. S. National Museum specimen here described is the only recognized example of the new species to which it is assigned. It also marks a new locality for fossil cycads in the Black Hills, having been found isolated by Dr. N. H. Darton, of the U. S. Geological Survey, about 4 miles west of Hermosa, South Dakota, where Battle Creek cuts through the Rim hills and cycad-yielding terranes. The trunk came from the north side of the Battle Creek Valley, and was unaccompanied by other silicified stems. It had remained wholly unnoted until Dr. Darton finally observed it entirely eroded out, after having at various times, in the course of several previous seasons, occupied in the study of rim stratigraphy, passed over the very hillside where it lay. In fact, Dr. Darton is of the opinion that the specimen could only have been eroded out within a year or two of the time when he found it, an opinion in which the present author gladly concurs, since he also passed along the "rim" and down over the very hillside where *C. Dartoni* later was found, on the morning of October 31, 1898, while engaged in a detour of the eastern rim in search of Cycadeoideas.

Cycadeoidea Dartoni, sp. nov.

1910. *Cycadeoidea Wielandii*, Coulter and Chamberlain. Morphology of Gymnosperms, p. 66, Fig. 55.
1911. (*Cycadeoidea turrita ?*), Wieland. Study of some American Fossil Cycads, Part V. Further notes on seed structures, Am. Jour. Sci., Vol. XXXII, p. 133 *et seq.*, Figs. 5, 6; also p. 458, Fig. 15 C.
1912. *Cycadeoidea turrita*, Wieland. Study of some American Fossil Cycads, Part VI. On the smaller Flower-Buds of Cycadeoidea, Am. Jour. Sci., Vol. XXXIII, p. 90, Fig. 11.

The trunk before us is from the same horizon which, 30 miles to the north at the Piedmont-Black Hawk locality and 35 to 40 miles southwesterly in the Minnekahta region, has yielded various columnar forms; but, as noted further on, it is a distinct species. It is with much pleasure that this wonderful fossil is named after its discoverer, who in the course of long studies of the stratigraphy and geology of the Black Hills Rim has also brought to light important forms of the associated Dinosaurian fauna.

Cycadeoidea Dartoni consists in the apical segment of a columnar trunk, the only portion recovered. The trunk segment tapers slowly to a small, well-conserved terminal bud and is much flattened, the greatest long and short diameters being 17 and 40 cm. It was broken off quite evenly and sharply 53 cm. below the summit, at about the point where apical tapering ceases and the full diameter is evidently reached. But as no initial basal curvature appears, and as the trunk may even have been markedly cylindrical, one may safely assign to the original fossil before broken in two in the process of erosion from its matrix, a height of not less than 1 meter. This is an unusually important measurement to establish in this instance because of the monocarpic habit of the species. For, as plainly to be observed in the plates and figures, the trunk bears all over its lateral surface a close-packed series of finely conserved cones deeply embedded in ramentum and leaf bases, and may with fair reason be held to have many claims to be not only the most remarkable of the Cycadeoideas, but perhaps even the most striking fossil plant that has ever been recovered in any country or any geologic horizon. See Plates 41–50.

Having first learned of the fossil from Dr. Darton, I was interested on visiting the U. S. National Museum a few days afterward to find that it was the trunk illustrated a year before in Coulter and Chamberlain's Morphology of Gymnosperms (1) as a specimen of *C. Wielandi* Ward, a species which bears abundant fruits, but which may or may not be monocarpic. Inasmuch as the authors just quoted only call attention to numerous strobili in the legend of the figure they give, it was a happy cause of surprise to find, from even the casual examination then made, that the "numerous" small-sized fruits literally fill the armor and must be present in the axil of every old leaf base, these hundreds of cones being in complete and fine conservation over all but about a third of the surface of the trunk, where some of the fruits had become granular in the course of time and are more or less completely worn away.

On being permitted, through Dr. Knowlton's accustomed helpfulness, to take a portion of the trunk for preliminary study, I selected, as least marring to the specimen, a small basal portion which was readily broken away. This, although covered with lime, evidently held the cones deeply embedded in ramentum and conserved out to their very tips. And so it proved on my return to the Yale Museum, the first section cut, a transverse one, revealing the fact that the fragment was made up of three entire and two less complete strobili with two of the five complementary leaf bases. This section is illustrated on Plate 45, photograph 1, and it seemed strikingly interesting to find that every seed contained a fairly well conserved dicotyledonous embryo.

Later, Dr. Knowlton had the entire trunk sawn through longitudinally, so as to divide it into as nearly equal parts as possible, the more sightly being reserved for exhibition in the United States National Museum, while the other was forwarded to the writer for sectioning and description. The segment illustrated in the natural size on Plate 43 was the one selected for this purpose. The interest with which the study of this specimen was begun at the Yale Museum may well be understood. For the first time in the course of fossil cycad study it had become possible to prepare the serial sections of surpassing beauty permitted by an armor packed full of finely silicified cones.

A true instance of culminant fructification or monocarpy—that is, growth of the parent plant to maturity and concentration of the entire reproductive force in a single season of excessive fruit production, followed by death—was never established among fossil plants until the present investigations were begun. Then, as recorded in Volume I, pages 128, 186, it was found that there was a very distinct tendency toward, if not actual culminant fructification in, such species as *C. Wielandi* and *C. dacotensis*, and that, since in *Cycadeoidea Stantoni* and *C. nigra* a series of peduncles occupied the axils of the entire old leaf-base series, these latter forms must have been monocarpic, no old peduncles having been at any time observed scattered about among groups of younger flowers in the case of any of the trunks studied with care. That such can occasionally occur is however indicated by the segment called *Cycadeoidea turrita*, bearing a single ovulate cone and shown on Plate V, photograph 2, Volume 1. (That specimen may be a younger *C. Dartoni* trunk.)

Later, on the appearance of U. S. Geological Survey Monograph LXVIII, it could also be observed, from the extended series of illustrations of Maryland cycads then given for the first time, that the great majority of the trunks of this striking columnar series could be divided into a larger group with few or no fructifications and a very similar if not specifically identical lesser group with fructifications apparently young occupying nearly all leaf-base axils. Of the latter type *C. Goucheriana* (Vol. I, p. 180, Pl. CV) is a striking example; while *C. marylandica* (Vol. I, frontispiece) and *C. Bibbinsi*, two very closely related forms,

fall but little behind in the abundance of fruits they bear. The series without fructifications is exemplified by the fine specimen of Figure 5, and by various other trunks and handsome trunk fragments with their leaf-base spirals undisturbed by the axillary fruits.

But although, so far as observation could go, it thus early appeared probable that the monocarpic habit or tendency was widespread in the *Cycadeoidea* alliance, it still remained necessary to an absolute proof to cut sections from a trunk bearing young fructifications in all the leaf-base axils, and to bide the "fortunes of the warfare" for the fortunate discovery of a trunk with the series of complementary fruits in a mature stage.

The first of these lacks was supplied by sections cut from material kindly supplied by Senator Capellini from the magnificent Italian trunk of the Capellini Museum of the University of Bologna, *Cycadeoidea Masseiana*. These reveal the young fruits in each leaf-base axil (390), fully confirming the earlier inferred resemblance to the Boulder cycad *C. nigra*, further described on a later page.

While it became evident enough that in Italy, in Maryland, in the Black Hills, in Colorado, and in California, these trunks of a monocarpic habitus must be characteristic members of the Cycadeoideæ, and doubtless could be conserved with all their fruits, none of the known localities gave much promise of yielding such an unique and marvelous fossil. But finally, as we now see, this last link in the chain of absolute evidence for a most-pronounced and extraordinary type of monocarpy in the Cycadeoideas has been supplied by Dr Darton's fortunate discovery of the trunk here described.

Having briefly called attention to the discovery and great interest of *Cycadeoidea Dartoni*, we may now pass on to a detailed description of the vegetative features and fruit series, illustrated on Plates 33–36, in part, and on plates 41–50.

The flattening of the trunk in the course of silicification has not markedly affected the appearance of the tissues under the microscope, being mainly evident from the ellipticity of the pith, wood zone, cortex, and armor without distortion of the wood tissues. That crushing has mainly affected the soft tissues of both the medulla and cortex first is, however, clear from the fact that, aside from the ellipticity of cross-section, the woody cylinder retains its proportions throughout, while the lateral region of the cortex is crushed out most, or least compacted. As the result of the compaction of the thick cortex, the leaf traces pass out from the woody cylinder almost horizontally at the point of greatest trunk curvature, but rise at a more and more acute angle on the flattened sides of the trunk. It is thus evident that the original angle between the woody cylinder and the general or average course of the cortical traces was intermediate between these extremes or approximately the angle to be seen about half-way between the middle of the flat side or trunk face and the middle of the most curved side, while the actual volume of the cortical parenchyma remains about normal despite deformation.

The *medulla* is not noticeably altered so far as its cellular aggregation goes, being simply flattened out rather than much diminished in its volume, which, as in the case of the cortex, can be little less than before crushing took place. Generally the medullar cell conservation is not good, especially toward the summit; though secretory sacs and canals with the contents very darkly stained are everywhere markedly abundant. However, since coloration and conservation vary so markedly in different parts of the stem, there must be some very considerable areas over which pith structures are as clearly differentiated as other tissues. (Compare Plates 43 and 44.)

The *woody cylinder* outlines can be seen with much satisfaction because of the complete longitudinal section through the trunk (Plate 43) and frequent transverse sections. As

evident in the plates, the xylem and phloem decrease steadily in thickness from 1.2 and 0.8 cm., respectively, below to about 2 mm. at the altitude of the last of the fruits, ending finally as mere strands supplying the undeveloped terminal helicoid of short bracts deeply embedded in their ramentum, best shown on Plate 42, photograph 4.

The wood, as in nearly all the Black Hills species, is primarily made up of scalariform tracheids. It is usually difficult to find other than the finely scalariform cells in the radial longitudinal section, though typical spiral forms do occur and there is some wood parenchyma. Next the medulla are the isolated strands of slender but thick-walled protoxylem cells. These pass up into the main body of the wood, which is composed all the way out to the cambium almost entirely of scalariform cells, with the typical ladder markings exhibiting frequent gradations into distinctly pitted types. That is, the typical scalariform sculpturing simply divides up into elongate oval, and finally the normally rounded and bordered Araucarian-like pits. The appearance is decidedly fern-like, and far more suggestive of *Cycas* than *Dion* with its more Araucarioxylon-like wood.

In the *transverse section* thin but well-marked growth rings occur to the number of about 25. The thinner-walled or wood parenchyma cells seen in the existing cycads are present, but there are no special features that have been as yet traced out. The usual alternating thin-walled and thick-walled cells make up the body of the phloem. On Plate 36, photograph 2, is given a section affording comparison with the wood of *Williamsonia*. Figure 36, opposite, shows the transverse section through xylem of quite exactly the same type of more or less angular tracheid with flat, squarish medullary-ray cells seen in *C. Dartoni*. These stems are closely associated with *Ptilophyllum cutchense* and other fronds in the Liassic strata of Amrapara, on the Bansloi River, Puchwara Pass.

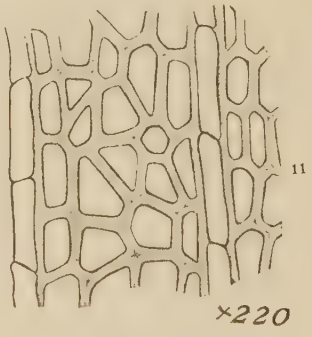


FIG. 36.—*Williamsonia* stem from India. ×220. From Bancroft.

The numerous *growth rings* are fairly conspicuous to the unaided eye, most so in the radial longitudinal section. Under the microscope the rings are far less pronounced, and found to be of the discontinuous type. This is seen in certain ancient woods like the Devonian *Callixylon Oweni* (80), and in some of the existing Araucarias. These rings are fully as pronounced as in the existing *Dion*. They may or may not be all seasonal, but it is of interest to find that just before the final burst of fructification the tracheids of the last few rings are noticeably large, indicating vigorous growth. Ring development is by no means so prominent as in several of the columnar trunks of the Piedmont-Black Hawk locality with the very heavy wood zone more comparable to that of *Cordaites*.

A more careful study of the radial sections so far available leads me to believe that the variations seen in passing from species to species of gymnospermous woods are little understood because no one has sufficiently studied the wood structure for the entire trunk in the case of any single form. There must be definite laws according to which the variations of cell types go on, some well-marked difference in the proportion of the various tracheid types in passing from base to summit of the trunk which is regularly coördinated with growth stages. The features of a few random sections cut at any convenient level must afford meager data for describing any wood type. Such sections are not located sharply with reference to any particular part of the woody wedges, and probably the so-called type sections of most woods so lack definiteness of position as to afford a very uncertain comparison with other forms.

The appearance of the radial section of *C. Dartoni* has just been described; and in the trunk of an Isle of Portland *C. megalophylla* a radial section about 10 cm. above the base has the same general characters. But just what these characters may mean in a random comparison with a radial *Dion spinulosum* section, where for a distance of 15 mm. all the tracheids have from one to three rows of pits, is not easy to say, for it is possible to go on almost indefinitely making such comparisons without reaching any very new or distinctly clear idea of wood structure in these forms. Thus in the Devonian *Callixylon Oweni*, in this same distance of 15 mm. the tracheids are all as profusely pitted; so also in *Agathis Bidwilli*, except that cells with sparse pitting are interspersed—merely the narrow ends or the more angular faces. On the other hand, in *C. Wielandi*, *Bennettites Gibsonianus*, etc., as it happens in the particular sections studied, for equally long distances only scalariform tracheids are seen, and in *Zamia floridana* only spiral forms occur. In the case of *C. Paynei* there is in the sections studied from the basal third of the trunk an easily recognized deep pitting or rather pit-like thickening of the medullary-ray cells of the xylem cylinder seemingly most abundant in the mid-xylem, but the final distribution of which in the different regions of the trunk, whether regular or irregular, is once more unknown. This feature is, however, by no means unique to *C. Paynei*. It is noted in lesser degree in the present and various other Cycadeoideans.

In short, the remarks to be found on page 76, Volume I, concerning the uncertainty of determinations and figures of wood structure based on random sections appear to be fully justified, and, accordingly, series of more exact studies of wood types in addition to the present have already begun. It is necessary to study the wood structures throughout entire wedges of certain of the best-conserved trunks like the present form and *C. Wielandi*, as well as several others, in the hope of reaching some satisfactory conclusion as to whether species may be determined from the wood structure alone. Obviously the *Cycadeoidea* stems peculiarly lend themselves to such an investigation. Requiring no staining, the saw-cuts may always be readily located, and the section records kept, while the thin woody cylinder must exhibit whatever change there may be in small compass. For one of these trunks is just as much a true tree trunk as is that of a pine or an oak. The large size of the pith, the often thick and pithy cortex bearing leaf bases which may or may not be persistent, may obscure the real form but do not constitute structures in any true sense different or remote from other stem types.

THE OVULATE CONE SERIES.

If there has ever been recovered any one fossil plant which more than all others might be signalized the most remarkable known, the present type must surely be the one. By careful estimate it is found to bear between 500 and 600 ovulate cones, the great majority of which are conserved in remarkable perfection and completeness. Only on the one flattened face of the trunk the armor is somewhat worn away so that a number of the fruits, perhaps half, are broken out over a considerable area, and the tops of others exposed or partially broken away. But even on this least perfect side of the trunk there are many complete fruits, a hundred or more, while all over the rest of the trunk, extending all the way from its broken base to the summit, the heavy ramentum is literally packed with the perfect and mature ovulate cones. Reference to the plates shows well these unique features wholly unparalleled among extinct seed-bearing plants. The cones occupy relatively the axils of all the old leaf bases, which latter are of but medium size and apparently somewhat excised, wilted, or even resorbed, being little conspicuous as compared with the cones in the large transverse sections. Remembering how exceedingly rare are fossil embryos, or other

structures comparable to embryos, such as may be observed at times in the seeds of the English "coal balls," it excites nothing short of amazement to find in the seeds of cone after cone the excellently silicified dicotyledonous embryos. (*Cf.* Plates 49 and 50.)

The cones of *C. Dartoni*, as naturally results from their great number, are of rather smaller size than the more isolated or only comparatively numerous cones of the nearly related species, such as *C. Wielandi*. At the base of the trunk segment the cones are 3 cm. long by from 1.2 to 1.5 cm. in diameter, with a peduncular length of 2 cm., this size gradually decreasing to the summit of the trunk, where the final cones have a length of only 2 cm. with a diameter of 1 cm., and are borne on peduncles but 1 cm. in length. The entire fruit series is a uniformly mature one; only a few lesser bract-bearing peduncles occur interspersed here and there among the full-grown cones. In a typical area of the armor a little larger than that of Plate 45, photograph 3, the cross-section reveals 22 axes, of which but two belong to the interspersed lesser series, which is best explained as abortive. It would be very singular indeed if this plant, in putting forth the tremendous reproductive effort involved in the production of a series of cones covering quite all its lateral surface, had not failed to mature a few of its axes. Some must inevitably have failed of growth.

There is, therefore, no evidence or indication of a monœcious condition. This plant was either diœcious or bisexual, with the chances greatly favoring the latter condition. An hypogynous shoulder with the wilted-down ridge of an earlier-borne disk is as prominent as in any other cycadeoid cones. That a functional staminate disk was earlier borne on these shoulders affords the best explanation of the condition found, although complementary evidence is awaited, it being somewhat singular that so far only a single axis of the present general type has actually been observed in a relatively young stage with the mature disk remnants still present (*cf.* Vol. I, Plate XLIII, phot. 7).

The probability that the true monocarpic condition here found illustrated in such a convincing manner must have characterized various of the Cycadeoideas, such as *Cycadeoidea Masseiana*, the great type of the Capellini Museum at Bologna, and the *C. Stantoni* of the Grapevine Valley, Colusa County, California, was emphasized in Volume I. In particular it was also pointed out that the conditions of fructification found in the Cycadeoideans indicate a widespread tendency to the monocarpic condition exhibited so strikingly, though in a much different manner, by the umbrella palm of Ceylon, *Corypha umbraculifera*.

The precise significance of monocarpy in the Cycadeoideæ is an interesting topic for discussion, but hardly germane to the present description; though it may be remarked in passing that this feature indicates the retention by these Liassic and Jurassic plants of the power to produce large numbers of fruits and shows that they, for this very reason, possessed in large measure their primitive plasticity. Each fruiting axis is first a branch, but more remotely each strobilus or disk is the analogue of an entire fertile columnar stem like that of a tree-fern, for instance. If, then, these cycads did not in some way retain as an inheritance the power of rapid fruit production, it must be said that they regained this power in a form quite capable of playing a new rôle in ecology and evolution. The Cycadeoideas can not, therefore, be regarded solely as large notably longevous and highly specialized types, stubbornly holding their place in the plant community. They could easily have had reduced herbaceous relatives with small flowers—annuals with the capacity to grow in great numbers, wilt down with the turn of the season, and form a rich, warm humus protecting numerous seeds and favoring germination in a succeeding rainy season or springtime; and any such plants would be the first to accommodate themselves to differential climatic change.

The seeds of *Cycadeoidea Dartoni* receive adequate description in the chapter devoted to Cycadeoidean seeds, so that it only remains to add that the general features of the type

trunk are not closely duplicated in any other specimen. It may be that, among some of the specimens referred to *C. Wielandi* or *C. McBridei*, younger examples can be found if search be sufficiently prolonged. The Yale cycad trunk 8 has some vegetative features in common, while the cone characters nearly agree, as will be observed on referring to the notes on *C. McBridei*. Now trunk 8 is merely a basal segment bearing the two isolated cones of Figure 22, and fruit growth near the base of *C. Dartoni* may have been quite as sparse. But the somewhat wilted leaf bases with the interspersed scale leaves of *C. Dartoni* can not be directly compared with the larger bases of Yale trunk 8. At best it seems a rather thankless task to eliminate, in a more or less dubious manner, or explain away, differences between *C. Dartoni* and the most nearly related forms that are more marked than those upon which at least one-third of all the European and the American species have been established. The difficulty of reference to any previously named species will be much better understood if attention be for a moment turned to Yale specimen No. 210, illustrated on Plates 39 and 40. This is the only trunk which appears to be a *C. Dartoni* cotype and has, in addition to a numerous fruit series, that completeness of preservation which makes adequate comparison possible.

Professor Ward, however, referred specimen 210 by number to *C. minnekahtensis*, evidently regarding the U. S. National Museum type as more freely branched than usual. This is doubtless the fact. Any of the branched robust trunks are both remarkable and exceptional. Seen from its unbranched side, trunk No. 210 has a marked resemblance to the *C. Dartoni* type, and in sections cut from a large cylindrical core the leaf bases and peduncles are found to agree well within all ordinary specific limits. But in addition to the tendency to branch, there is a further difference in the presence of two series of ovulate fruits, one large and few in number with large seeds, and the other a very numerous lesser series of young forms, mostly ovulate so far as seen, but as yet insufficiently studied. Ultimate study may therefore show that it would have been wiser to make a provisional reference to *Cycadeoidea McBridei*, although this species is in turn of somewhat uncertain boundary. In any case Yale trunk 210 is the visible link between the columnar and branching cycadeoids and shows how a scattering series of fruits could occasionally precede a final profuse fructification.

If, then, it be difficult to find among well-conserved trunks an exact counterpart of the U. S. National Museum type, the more can it be appreciated how doubly difficult, in the present stage of fossil cycad study, it is to identify surely those more fragmentary trunks lacking their full fruit series. There appears, therefore, to be but one logical and practical method of procedure, and that is to assign this splendid specimen to a new species, as is here done. Generally speaking, the American species are all founded upon the most perfect specimens, and this is by far the most practical method of procedure, the one which, if consistently pursued, will lead to final and satisfactory accuracy.

It is desirable to establish the specific series for these cycads—and easily practicable, if botanists and paleobotanists will only bestow the necessary meed of discrimination and patience. With Professors Marsh and Williston, one can readily agree that all fossil types should, as far as possible, be based upon the most perfect specimen obtainable. For only so may we lighten the work of classification—far more necessary than is sometimes appreciated. Accordingly, so long as the remotest doubt as to the characters of imperfectly known types exists, the burden of proof should rest upon the least-known species and when new specimens are found of fine conservation and exhibiting remarkable assemblages of characters, they should receive new specific names unless it can be convincingly shown that they belong to and merely extend our knowledge of more imperfectly known species.

Doubtless this principle is already widely admitted in practice, though desirable to restate in the present connection. It is here doubly necessary to avoid, as much as possible, the inconvenience that reference of well-conserved trunks to little-known species always sooner or later involves, since the more striking forms receive such great prominence and very frequent mention. When the types are conspicuous it is easier to simplify the catalogue or other completer lists and at once indicate the points where further study may begin. In fact, it would be an even better practice to avoid any specific reference for the great majority of lesser specimens, setting them aside or referring to them by number until such time as they may be indisputably named.

Furthermore, the day may come when, as the result of persistent and methodic collection of fossils, specific names will become so burdensome in number as to break down the binomial system; if so, it is certain that some numerical system permitting a free shifting from end to end of the generic series will be adopted; but until that day arrives a certain convenient elasticity of the binomial system may best be had in the manner indicated. These ideas have already received some attention in the introductory pages, but easily bear a partial repetition in connection with the present striking instance of their application. There is scarcely a single fossil plant type where the hiatus between the least-known and the best-known species is so great as in the case of the Cycadeoideans, and no one will have fully grasped the real significance of Cycadeoidean species who does not keenly realize the fact that this gap is being widened every day. In no other group of fossil plants is the opportunity for progressive study so great as in the Cycadeoideæ, the type before us being a patent example of a species which can be studied with profit almost indefinitely, even without the discovery of additional examples in varying stages of growth and fructification. Comparably speaking, how slight indeed is the gap between the least-known and best-known species of a genus or of a family of Ammonites, how relatively small the possibility for progressive study of the best-known species.

FIG. 37.—*Cycadeoidea Dartoni* (?). Yale trunk No. 210. Section 851, ×20. Transverse section of one of the young and small crowns of fronds borne by the axis marked II, Plate 39, and in part illustrated in Plate 40, photographs 4, 5.

Observe the *Otozamites*-like ears of the pinnules as indicated by the arrow. Only an eared pinnule could be so cut, it being further clear that the plane of the section must pass beneath the insertion of the pinnule to which these ears respectively belong. Evidently they belong to one and the same pinnule.

YOUNG FRONDS.

As above explained, the terminal bud of the U. S. National Museum type is entirely composed of scale leaves thickly enveloped in ramentum, and no traces of adventitious leaves have been found. In the case of the possible cotype Yale trunk No. 210, there is much more promise of leaves being concealed in the terminal bud, the sectioning of which remains to carry out. However, there are a number of very conspicuous axes scattered about the upper third of the trunk, which were at first thought to be bract-enveloped fruits

of larger size, but which prove to be vegetative axes bearing some very young fruits laterally and terminating in small crowns of very young fronds. Although these fronds are but little larger than the bracts inclosing the ovulate fruits, and so minute that they can only be well seen under the microscope, it does not seem necessary to regard their well-formed pinnules as mere appendages of scale leaves. They are much more than this, as Figure 37 plainly shows. The axis from which the section 851 was cut is denoted in its original position on the trunk on Plate 39 (II). It was drilled from the trunk in the form of a cylindrical core, and structure details below the level of the section cutting through the fronds are illustrated on Plate 40, photographs 4 and 5. The comparison of such axes with the scaly buds of *Cycas* is at once obvious, but it is the young fronds that now deserve attention.

Whether or not the fronds like that here illustrated reached any considerable size, such, for instance, as a third that of the mature fronds of the crown, the considerable number of the pinnules (11 in one rank and 12 in the other), the pinnule insertion, and the form of the rachis, must surely indicate the essential features of mature fronds. Even as fossilized there are very distinct indications of the pinnule bundle position and venation, and it may be fairly inferred that the pinnules of the fronds crowning the trunk were numerous—anywhere from 25 to 75 in number. Similarly, it is evident that the full-grown pinnules were broad rather than linear and acuminate; that they were not inserted in a groove so marked as that in most modern cycads, and that finally they were eared as in *Otozamites*, so profusely exemplified in the Mexican Liassic. This last is a very important point, since eared pinnules have never before been observed in the silicified series of cycadeoids and do not occur among existing cycads, although so universally present in the Jurassic. Evidently, since both eared and more *Podozamites*-like silicified pinnules occur, it may yet prove possible to divide the *Cycadeoidean* fronds into several groups, perhaps of generic or semi-generic value, quite comparable to the arbitrary frond genera of the closely related Williamsonian tribe.

FIG. 38.—Typical transverse and longitudinal sections of *Cycadeoidea* or *Cycadella* trunks from Freeze Out Hills of Carbon County, Wyoming, now in collections of U. S. National Museum.

A.—*C.* (*Cycadella*) *wyomingensis*. (×0.4.) Transverse section of trunk with crushed, more or less macerated medulla and partly collapsed woody cylinder. Armor well conserved.

B.—Longitudinal section of another *C. wyomingensis* trunk crushed similarly to the preceding. (×0.4.) U. S. Nat. Mus. Nos. 500, 681. Weight 11.34 kg. (Mentioned at length on page 184, U. S. Geol. Surv. Mon. XLVIII.)

C.—*C.* (*Cycadella*) *nodosa*. (×0.65.) Cotype No. 100, 206 figured on Plate LI, U. S. Geol. Surv. Mon. XLVIII. Longitudinal section revealing unusually heavy wood zone. Weight, complete trunk 2.8 kg. *Cf.* text.

D.—*C.* (*Cycadella*) *wyomingensis*. (×0.65.) Longitudinal section through another trunk of the type series (No. 500, 14) weighing 12 kg. The entire trunk is figured on Plate LXXXI, Part II, Report XX, U. S. Geol. Surv. The trunk appears to fork, but on the basis of the median section alone beware of "crows' nests"!

CHAPTER VIII.

THE FREEZE OUT HILLS GROUP OF TRUNKS.

The close association of Sauropodous Dinosaurs and silicified Cycadeoids in the Como or Atlantosaurus beds of Marsh, now included in the Morrison formation, in east-central Wyoming, was first observed by W. H. Reed and brought to scientific notice by Professor Marsh, as below recorded. The Morrison formation outcrops nearly all round the Black Hills full 200 miles northeast of Carbon County, Wyoming, and at least on the west side of the Hills scattering trunks have been found (Wieland, 1905) like those so abundant further west. The eastern Wyoming fossil cycad region is thus extensively overlain by the main Black Hills fossil cycad terrane of the lowermost Lakota. It is the third and last of the greater American localities to be discovered, representing a very extended cycad-bearing area which has already yielded a long list of specimens comparable in importance with those of other notable localities like, for instance, that of the Isle of Portland. Hundreds of specimens have been collected in the Freeze Out Hills, 25 miles due north of Medicine Bow.

The Freeze Out Hills Cycadeoids constitute a strictly pygmic series with uniformly profuse ramentum. The trunks seldom exceed 25 kg. in weight, being mostly small oblong cylindrical to slightly columnar plants, which may have grown on dry, rocky hillsides rather than in Monsoon forests. Thus far only occasional evidence of branching has been found, though lesser scale-leaf buds are evidently present and the infrequency of branched trunks is probably due to the fragmentary character of so many of the specimens. As explained in Volume I, notwithstanding some evidence of maceration and much compression, conservation is in nearly all cases exceedingly good. Only because of the lesser size of the trunks and their frequently crushed and broken condition do they fail to yield the handsome longitudinal and transverse sections afforded by the larger Black Hills specimens, which doubtless offered more resistance to compression or were more favored during the early stages of fossilization. But this crushing does not interfere at all with histologic study, while the smaller size of the specimens and the many fragments of trunks markedly favor sectioning. For some reason or other very few fruits have been found conserved. Perhaps mainly because the trunks grew so near the surface of the ground the peduncles tend to somewhat greater relative length than in the case of larger trunks; while, just as might be expected, where the peduncles tend to greater length they are fewer in number. Also, there is a frequent droop in the armor, such as may be observed in some of the Isle of Wight specimens, the ramentum of leaf and peduncle bases hanging down over, and more or less concealing, the leaf-base ends.

Cycadeoidea (Cycadella).

1898. MARSH. Am. Jour. Sci., 4th Ser., Vol. VI, pp. 115–116. (Records discovery of new locality and receipt of two specimens at Yale Museum, later made the types of *Cycadella Reedii* and *C. Beecheriana.*)

1900. WARD. Proc. Wash. Acad. Sci., Vol. I, pp. 253–300. Pls. XIV–XXI. (Description of a New Genus and twenty New Species of Fossil Cycadean Trunks from the Jurassic of Wyoming.)

1900. WARD. Jurassic Cycads from Wyoming, in Status of the Mesozoic Floras of the United States. First Paper: The Older Mesozoic. Extract, Ann. Rep. U. S. Geol. Surv., Vol. XX, Pt. II, pp. 382–417, Pls. LXX–CLXXVII. (Same as preceding, with addition of long series of plates illustrating quite every specimen earlier secured except one collected by Williston for the University of Kansas at Lawrence and an excellent lesser collection made by J. B. Hatcher for the Carnegie Museum at Pittsburg.)

1905. WIELAND. On the Foliage of the Jurassic Cycads of the Genus *Cycadella*. U. S. Geol. Surv. Mon. XLVIII, pp. 198–203, Pls. LXII, Figs. 1–3, Pl. LXIII, Fig. 1. (Describes ramentum structure and finely conserved adventitious leaves of trunk designated as type of *Cycadella wyomingensis*.)

1905. WARD. Jurassic Cycads from the Black Hills. U. S. Geol. Surv. Mon. XLVIII, pp. 203–204. (Refers to locality and horizon of isolated southwestern Black Hills stem called *Cycadeoidea utopiensis*.)

1905. WIELAND. Field Notes in U. S. Geol. Surv. Mon. XLVIII, pp. 205–207. (Records occurrence of *Cycadella* on western side of the Black Hills.)

1905. WARD. Jurassic Cycads from Wyoming, U. S. Geol. Surv. Mon. XLVIII, pp. 179–198, Pls. XLVI–LXI. (Illustrates and describes an additional consignment of Freeze Out Hills specimens, including a few fairly complete trunks and a large number of small fragments numbering over 500 pieces.)

1906. WIELAND. American Fossil Cycads, Vol. I, pp. 8, 9, 53, 63, 167, 175–176, Figs. 21, 53, 93, 18, 35, Pl. XVII, Phot. 3, and Pl. XVIII. (Gives various notes on features of the Wyoming group, with detailed description of leaves of *Cycadella ramentosa*, pp. 100–102, and young bisporangiate strobilus of *Cycadella wyomingensis*, pp. 175, 176.)

With a single possible exception, apparently indicating a polyxylic cylinder to be further mentioned below, the Freeze Out Hills trunks represent a characteristic and homogeneous series; and this fact, taken together with the presence of occasional masses of ramentum drooping from the peduncles or the outer bracts borne by them, led Professor Ward to assign this assemblage to a new genus, *Cycadella*. But while it should by no means be considered that this new genus is finally and absolutely overthrown, it is, definitely speaking, necessary to recognize the fact that up to the present hour no features have been found in the case of any single specimen referred to *Cycadella* which are not found duplicated over and over in characteristic Cycadeoideas. That is, generically speaking, no sufficiently sharp variation in general trunk form, wood structure, leaf-base structure, leaves, or fruits has been found on which to base a separation. True enough, knowledge of the fruits is so far limited to almost a single small and young bisporangiate strobilus observed in *Cycadella wyomingensis* (*cf.* Vol. I, p. 175, fig. 93). However, the usual campanulate disk being present, generic separation on the score of unknown fruits is not permissible, and as the case stands a point has been reached where the burden of actual demonstration of structure generically different from *Cycadeoidea* prevents retention of *Cycadella* as a well-established genus. All the forms referred to it must, in fact, be considered as members of the cosmopolitan genus *Cycadeoidea* and it only remains to make some notes on the species represented as a preliminary to the later and more careful histologic study which the Wyoming group deserves.

To the genus *Cycadella* Professor Ward ascribed an even score of species in the following order, which should be recorded because upon it must depend all questions of specific priority which may at any time arise:

1. C. Reedii	6. C. jurassica	11. C. ferruginea	16. C. concinna
2. C. Beecheriana	7. C. nodosa	12. C. contracta	17. C. crepidaria
3. C. wyomingensis	8. C. cirrata	13. C. gravis	18. C. gelida
4. C. Knowltoniana	9. C. exogena	14. C. verrucosa	19. C. carbonensis
5. C. compressa	10. C. ramentosa	15. C. jejuna	20. C. Knightii

The first two of these types, a small bulbous trunk or branch, and a somewhat larger columnar form about 30 cm. high, are in the Yale collection. The remaining 18 types belong to the museum of the State University of Wyoming at Laramie. In addition a considerable number of duplicates, so designated, are included in the Cycadeoid collection of the U. S. National Museum at Washington. These latter, with the two Yale specimens, have constituted the chief source of material on which I have depended in my study of the Wyoming cycads; but many fruit nodes and armor portions of the original types have also been examined or sectioned. In particular the leaves and the young fruit above mentioned are from the figured specimens of *C. wyomingensis*. In addition, through the kindness and coöperation of the officials of the U. S. National Museum, a series of representative longi-

tudinal and transverse trunk sections have been made preparatory to a reasonably thorough histologic study of the Wyoming species. Photographs of four of these trunk sections, very kindly made for this volume by Professor R. S. Bassler, are shown in the accompanying text-figure 38.

While it is, therefore, much too early to attempt any final pronouncement on the precise identity and actual number of the Carbon County species, a very fair general statement may be made. From the examination of material made along the lines just mentioned it has become reasonably certain that not more than four distinct species are included in the entire series of trunks. It is, of course, possible that the fairly large specimen collected by Professor Williston and now in the Museum of the State University of Kansas at Lawrence, or some of the Carnegie Museum specimens collected by Hatcher, which I have not as yet seen, may include a distinctive form. In fact, a group of some half dozen trunk fragments sent to me by Professor Knight includes a form with rather the largest leaf bases yet observed in the Wyoming series. But on the whole, after handling several hundred specimens, both complete and fragmentary, it not only seems most unlikely that more than four species can be found, but I am led to suspect that ultimately the actual number may be reduced to three or even to two forms. Many of the specimens must be referable to the *Cycadeoidea utopiensis* of the southwestern Black Hills, which has priority over the Wyoming series. The longitudinal and transverse sections necessary to the completer study and comparison of this type have not yet been made, as it was not at first realized that the Carbon County series would prove so lean in species and that this trunk would come to have so much relative importance. An armor section is given in Volume I, figure 21.

It may be said that a macroscopic determination of the Wyoming cycad species has not proven feasible. The supposed distinguishing characters are soon found to shade into imperceptible differences. Apparently resting under the impression gained from the Black Hawk group, in which specific indices are varied and striking within the close-set limits of columnar trunk form, Professor Ward here gave too little weight to the extreme difficulty of determination from macroscopic characters. Even in the case of the Black Hawk specimens, could he have more closely scanned the series aided by various polished trunk sections, doubt as to specific boundaries would have grown sharper as the extensive variation in outer appearance due to scale leaves became more and more apparent. The real interest of the Wyoming group is therefore biologic, and the early enumeration with illustrations extending to nearly 200 octavo plates retains simply a catalogue value in displaying so fully and thoroughly the large amount of excellent material resulting from only a few years of casual collecting. An adequate idea of what this mass of material really means may best be had by visiting the habitat of the Florida Zamias, or, if that be inconvenient, by securing and unpacking a barrel of the *Zamia* trunks as gathered at random in the pine woods. Some of the variations observed in a series of trunks so collected are recorded in the notes on *C. excelsa*. Fructifications are even less abundant than in the Isle of Portland series.

Temporarily an ascription of the Wyoming specimens might be somewhat arbitrarily made as follows:

1. For small bulbous trunks, *Cycadeoidea* (*Cycadella*) *Reedii*.
2. For rather slender columnar trunks, *Cycadeoidea* (*Cycadella*) *Beecheriana*.
3. For low-growing robust trunks, *Cycadeoidea utopiensis*.
4. For the largest stems, *Cycadeoidea* (*Cycadella*) *wyomingensis*.

Inasmuch as the literature relating to the group has already been cited in full, it is not necessary to restate references to the wholly arbitrary descriptions of even these four

species. They will be further studied and doubtless will be found to very adequately represent the Wyoming series. It may be added that one specimen and one only shows any indication of growth rings or of a polyxylic condition. This is the small trunk weighing between 2 and 3 kilograms figured on Plate LI, U. S. Geological Survey Monograph XLVIII, as a *Cycadella nodosa*. The longitudinal trunk section shows three xylem divisions at the base, each about 0.5 cm. in thickness. But even if thin sections should later show absence of crushing zones with presence of three cambial zones and a true trixylic cylinder, there would be no further reason for separation from *Cycadella Reedii;* for an isolated case of partial polyxyly might well occur among such a large number of trunks and thus only have structural interest. The longitudinal trunk section, which is shown in Figure 38 A, was only recently cut and supplementary thin sections have not yet been prepared.

It would, of course, be easy to go on from this point and cite a number of pages of notes on the U. S. National Museum specimens in support of the contention that the fine assemblage of Wyoming cycads includes no more than two or three species. These are at hand with references to the numbered specimens of interest in illustrating the group and comparing with other forms. But these notes would add nothing of present use to the general statement just given. Instead of incorporating such details it may suffice to add that in suggesting a more or less provisional reduction of the specific list of 21 to 4, to 3, to 2, or to but a single species, there is no need to lose sight of the fact that some rarely extended series of these trunks, illustrating all stages of fructification and all features of mature fronds and fruit growth, might well exhibit a wider range of specific variation. Accordingly, the more or less arbitrary division of such a group of fossils as that under consideration into a specific series often has in its favor a certain large and by no means wholly negligible element of chance. In fact, this element of chance becomes so great, when comparison is made between fossil forms nearly but not absolutely alike and separated widely in either latitude or time, that it can not be ignored. There is, therefore, no rule of thumb to aid the paleobotanist; his species may rest on differences either less or greater than those upon which species of living plants are ordinarily founded.

CHAPTER IX.

ISOLATED TYPES FROM COLORADO, CALIFORNIA, AND TEXAS.

Cycadeoidea mirabilis (Lx.) Ward.

Zamiostrobus ? mirabilis, Lesquereux. Bull. U. S. Geol. and Geogr. Surv. Terr., Vol. I, 2d ser., No. 5, p. 383, 1875 (1876); Tert. Fl. p. 70. Pl. XLIII, Fig. 1, 1878.
Nelumbium, James. Science, Vol. III, p. 434, 1884.
Clathropodium mirabile (Lx.), Ward. Science, Vol. III, p. 532, 1884.
Cycadeoidea Zamiostrobus, Solms. Mem. Real Accad. Sci. Ist. Bologna, Ser. V, Tom. II, p. 210, 1892.
Cycadeoidea mirabilis (Lx.), Ward. Proc. Biol. Soc. Washington, Vol. IX, p. 86, 1894.
Cycadeoidea mirabilis (Lx.),Ward. Bull. U. S. Geol. Surv., No. 152 (Knowlton's Cat. Cret. and Tert. Plants), 1898.
Cycadeoidea mirabilis, Wieland. American Fossil Cycads (Structure), p. 7, 1906. Locality near Golden, Colorado. Exact horizon unknown, but doubtless equivalent to the upper *Cycadeoidea* horizon of the Black Hills Rim.

Inasmuch as the type of *Cycadeoidea abiquidensis* Dawson, from the Permian of Prince Edward Island, named in 1871, is a cast with little indication of the original structures, the finely conserved trunk fragment which Lesquereux called *Zamiostrobus mirabilis* is chronologically of much importance. In fact, at the time of its description (1876) no specific name had been applied to any closely related specimen from this continent. Not until thirteen years later was the first Maryland species, the "*Tysonia marylandica*," described by Fontaine; while the Kansas specimen *C. munita* of Cragin also dates from 1889, and *C. Jenneyana*, the first described of the Black Hills specimens, follows four years later.

Furthermore, in 1876 the Italian species *Cycadeoidea etrusca*, *Ferrettiana*, *Capelliniana*, *Maraniana*, and *Masseiana* had not been named, while other later European species are *Cycadeoidea Niedzweidskii* Raciborski (1893), *C. micromyela* Lignier (1901), and *C. Fabre-Tonnerrei* Lignier (1910), and the interesting series of trunk casts described from the Albien-Cenomanien of the Argonne by Fliche (1896). Some of the comparable forms described by Saporta (1875) as *Bolbopodium* have a much smaller medulla.

Thus all American and most European forms nearly resembling *C. mirabilis* are of later date than 1876; and it is also certain that some years of study and comparison will be required before any final pronouncement on the characters of related older types can be made. Even were the Colorado type well known in all its structures, the likelihood that any present specific names would be affected is exceedingly small. In fact, even the gross features of the earlier-named European types fail to suggest specific identity with the Lesquereux type. The European specimens which more broadly suggest relationship are the later-named *C. Capelliniana* and *Maraniana*, and Lignier's *C. Fabre-Tonnerrei* (155).

Through the courtesy of Dr. F. H. Knowlton, of the U. S. National Museum, I have been permitted to photograph the original type of *Cycadeoidea* (*Zamiostrobus*) *mirabilis*, and also to set aside for microscopic study a small but good wedge cut away at the time the specimen was loaned to Count Solms. His notes are to be found in the Capellini and Solms account of the Italian cycads (48). Accordingly, I at present give directly from the original specimen, and without reference to any previous descriptions, a brief account of the macroscopic features of this first named of all North American trunks with structure conserved.

The *Cycadeoidea mirabilis* is a solidly silicified fragment from one side of the upper region of a medium to small-sized columnar trunk. The specimen is of broad, flattened-wedge shape, lacking the medullar edge, which is mostly broken or eroded away; it is 12 cm. broad, 4.5 cm. high, and includes a scant third of the estimated trunk circumference.

The armor, cortex, and wood zone are very well defined, as reference to Plate 1 shows. The trunk was slightly flattened, although the greater diameter could not have exceeded 20, or the lesser have fallen short of 15 cm., while the curvature indicates a columnar rather than a low or distinctly spherical stem. But this habitus might be expected from the fact that the Black Hills trunks with about the same general features are likewise flattened and columnar.

Armor.—The outer surface of the armor is of a peculiar gray jaspery to slightly reddish tinge, making it difficult to photograph the leaf-base pattern, which is, nevertheless, wholly distinct. Hence, in order to secure a good photograph of the armor surface, the ends of the leaf bases were carefully brushed with India ink. But the fact that the specimen was so treated would not be obvious from the reproduction (Plate 1, phots. 1, 3), the jaspery and black colors having nearly balanced each other on the original negative. The leaf bases as eroded do not show their bundles, but the moderately developed ramentum is seen to be unusually fine to hairlike. The armor is 3 cm. thick, and it is very noticeable that an excising layer of periderm had developed more or less regularly about 1 cm. beneath the leaf-base ends.

Cortex.—The cortex is no more than 4 mm. in thickness, and the leaf traces, although clearly of the horse-shoe type usual in the Cycadeoideæ, are the smallest observed in any trunk so far studied.

Wood zone.—The moderately developed wood zone, 13 mm. in thickness, has a compact *xylem* exactly 1 cm. thick, traversed by numerous growth-ring-like bands; these tend to hold a quite even distance apart, and must be due to growth rings, as in some of the Black Hills trunks. The woody wedges are regularly 5 mm. broad, in conformity with the small and numerous leaf bases. Taking the armor measurement of 3 cm., cortex 4 mm., phloem 3 mm., xylem 1 cm., and the estimated least and greatest trunk diameters at 15 and 20 cm., the diameter of the *medulla* appears to have been from 6 to 10 cm.

Fructification.—Several areas readily noted in the photographs clearly show what must be buds with the very young fruits concealed within; but more conclusive is the presence of a small bract whorl in the wedge to be studied later, which will doubtless show all that can be learned from a specimen evidently young and with few incipient fruits.

Possible synonyms of Cycadeoidea mirabilis.—Among the Freeze Out Hills types as yet histologically unstudied there may well be included trunks which it will ultimately be found necessary to refer to *C. mirabilis*. In the case of the Black Hills trunks no example has been found so far. One of the most nearly related forms is the trunk numbered 377 in the Yale collections. This specimen, as represented on Plate 30, photographs 2–4, has the same general columnar form and much the same development of armor and narrow cortex, but can not be of the same species, as the wood zone is only from 5 to 7 mm. thick and about equally divided between xylem and phloem, while the cortical bundles are, on the contrary, relatively large, not small. This trunk, No. 377, is also only a fragment, but even were it possible to compare the entire woody cylinders of both fossils, such wide differences would scarcely be expected in one and the same species. Such variable proportions doubtless constitute the best of specific indices.

For any attempt at comparison with *Cycadeoidea nana*, to which certain young or small-sized specimens from Minnekahta have been assigned, the necessary series of sections is not yet at hand. It may, however, be mentioned that none of the Black Hawk species agree. The *C. rhombica* is nearest with equally small and regular leaf bases, but there is far less development of ramentum and a very large medulla.

Cycadeoidea Stantoni Ward.

1905. WARD. U. S. Geol. Surv., Mon. XLIX, pp. 273–277, Pl. LXX.
1906. WIELAND. Vol. I, p. 185.

The Cycadeoidea obtained by Dr. T. W. Stanton in Colusa County, California, at the ranch of Mr. B. P. Pryor, in the Grapevine Valley, 6 miles west of Sites, on the road to Stony Ford, is in many respects an interesting specimen. Especially its isolation makes it desirable to recover, if possible, other examples or associated species. Because of this fact it is desirable to quote Dr. Stanton's account, as follows (Ward, 362, p. 273):

"The specimen was in the front yard at the ranch house and Mr. Pryor says it was there when he moved to the place several years ago, the previous occupant of the house having been his uncle. He is confident that it was picked up in the field near by, and he showed me another cycad fragment, badly weathered, that had evidently formed part of a large specimen, stating that he himself had found this specimen in his plowed field. There were also fragments of rock with lower Chico invertebrates that had been picked up in the same field, and he directed me to a locality near by, on beds whose strike would carry them up the valley through this field, where Chico fossils were found in place.

"The valley of Grapevine Creek is here not more than one-fourth to one-half mile wide and nearly parallel with the north-south strike of the strata exposed in high ridges on either side. A short distance up the creek (south), however, its course changes so that its source is some miles to the westward, and it probably crosses both Knoxville and Horsetown beds, though no direct paleontologic proof of this was found. Assuming that the cycad was brought to Pryor's field a greater or less distance by Grapevine Creek, the possible sources of the specimen seem to be limited to the Knoxville, the Horsetown, and the lower Chico, with the probabilities in favor of one of the two last named.'

The general characters and surface features of the *C. Stantoni* type are quite exactly described by Professor Ward. The armor is well conserved on one side only, its most striking feature being the series of bract-surrounded peduncles occupying all the leaf-base axils. The bracts are relatively large and seem to close in over the tops of the old peduncles of lesser size. This specimen, therefore, belongs to the columnar monocarpic group represented by the Italian *Cycadeoidea Masseiana*, the Black Hills *C. Dartoni*, and the Colorado trunk *C. nigra* further mentioned in the succeeding description of this latter species. Although a trunk wedge is not yet available for the study of histologic features, the Colusa type should be arbitrarily held specifically distinct from all of the species just named. The outer appearance varies sufficiently to justify this. It is possible, however, that there is a further or even a fairly close resemblance to *C. marylandica* or to the Texas *C. Uddeni*, although the latter two species are not truly monocarpic. The flowers of the Colusa type probably projected beyond the armor and may never be found. However, it seems that any small and projecting or pendent floral types would be more subject to variation in form than the large flowers more closely packed in the armor of other species. Conjecture as to the floral features must therefore rest partly on such discoveries of Williamsonian flowers as may from time to time be made. There is as yet no sufficient ground on which to include this type in a new genus, but the possibility that it is generically distinct may better receive mention in the description of *C. nigra* succeeding.

Cycadeoidea nigra Ward.

1900. WARD. Rep. U. S. Geol. Surv., XX, pp. 377–382, Pls. LXVIII, LXIX.
1906. WIELAND. American Fossil Cycads, Vol. I, pp. 7, 12, 22, 52, 33, 60–64, Figs. 31, 33 (3).

About 1885, as related by Professor Ward, a certain J. Alden Smith secured, during the excavation of a railroad cut near Boulder, Colorado, the segment from the mid-region of a tall *Cycadeoidea* which constitutes one of the most important of all American types, *C. nigra*. It appears that this specimen was reposed without description in the exhibition collections of the State School of Mines at Golden. At least it was not until 1896 that

Dr. Knowlton chanced to observe the specimen and direct the attention of Professor Ward to its interesting character. At the time it was found other parts, so the workman said, had been covered up in the dump; and one must believe this statement correct, for the type segment is obviously from the mid-region of a tall columnar trunk. It is 40 cm. in height, and not crushed, although, like so many Cycadeoideas, compressed without distortion. Moreover, while silicification is most perfect throughout and the armor surface unweathered, both ends terminate in the freshly fractured hard black silica.

Professor Ward (359, p. 379) somewhat doubted the information given Dr. Knowlton that the original trunk was "two or three times as tall" as the recovered segment; but the least possible length of the entire stem must have been close to 1 meter, and there is really no visible reason why such a trunk may not have reached a height of even 2 meters. Certainly the trunk would have been sharply over a meter in height if it had the habitus of the columnar *C. Dartoni*. But the height of that specimen also being conjectural, there is as yet no means of estimating the extreme height reached by columnar forms of monocarpic habit. It might, however, be suspected that *C. Dartoni*, with such great numbers of fruits packed in the armor, would not tend to reach as great a height as a form like *C. Stantoni* or the present type with long slender peduncles bearing pendent flowers.

The dense texture, strong tendency to conchoidal cleavage, and even black color of the Boulder specimen afford the appropriate specific name. Because of this almost coal-like texture, the surface details are somewhat obscure, despite the fine conservation. They are, however, described by Professor Ward with such accuracy that no further repetition is required. The armor where least compressed is 6 to 7 cm. in depth. In Volume I the transverse section of the armor traversing the leaf bases and axillary peduncles with their bracts is figured. The important fact disclosed by the sections is that the thick armor does not conceal fruits; only the rather small triangular peduncles surrounded by five or six of the more basal bracts are present. The bracts are in transverse section distinctly crescentiform with the horns rounded, and are nearly as large as the peduncles. The type segment of *Cycadeoidea nigra* has recently been forwarded by its conservators to the U. S. National Museum for the completer study which should be given to the wood zone. The preliminary saw-cuts now made show this to have all the interest anticipated. The cortex is thick, and the medulla, about 2 cm. in diameter, proves the smallest yet seen in a columnar form.

The discovery of *C. Dartoni* invited attention anew to the Boulder cycad, the group of columnar monocarpic trunks now having become an impressive one. It will have been observed that of the four Cycadeoidean trunks with peduncles in all the leaf-base axils—namely, the Italian *C. Masseiana*, the Hermosa trunk, the Colusa trunk, and the present type—the two latter have slender peduncles, while the two former have short, heavy peduncles. In *C. Dartoni* the armor is packed with fruits and in *C. Masseiana* it is probable that the same condition obtained, although the fruits of the type are young. If these several forms were associated in the same beds and more strongly resembled each other, one might well be inclined to regard the two forms with slender peduncles and pendent flowers as staminate, the two with the armor packed full of ovulate cones as the complementary seed-bearing trunks of a dicœcious group. Indeed, since it is not proven that *C. Dartoni* was bisexual or monœcious, one might well picture for that species such a dicœcious habitus.

But it must suffice to simply bear in mind these interesting possibilities. It is not likely that any one, with all four of these trunks before him or borne well in mind, would fail to assign them to different species, and the precise significance in the specific or generic scheme to be attached to the long peduncles of *C. Stantoni* and *C. nigra* must be determined

later. There might, however, be nothing in the way of segregating these four tall monocarpic trunks as one of the several genera into which the Cycadeoideæ are ultimately destined to be split, although this would be contrary to the conservative method followed in carrying out the present taxonomic studies. The *Cycadeoidea Reichenbachiana* is also columnar and monocarpic, but with the far larger fructifications relatively few in number and resembling those of the great branched trunks from Minnekahta. It is a singular coincidence that the five most conspicuous examples of monocarpic trunks are from such widely separated regions as Galicia, Italy, Dakota, Colorado, and California, in each instance but a single specimen having been recovered. Is there not here a strong incentive to the collector to revisit and examine with the utmost care these several localities? As yet the *C. Dartoni* is the only trunk of the monocarpic group to be discovered by a competent collector where eroded out.

Cycadeoidea Uddeni (sp. nov.).

By far the most recent member of all the Cycadeoideæ thus far discovered is the type of the present species. It consists of three pieces of the armor of what was in life a heavily armored ovoid trunk about a foot in diameter and a foot or more in height. This interesting specimen was found high up in the Upper Cretaceous of Maverick County, Texas, by Professor J. A. Udden, who gives the following account of the locality and horizon of this type which is now in the Yale collections:

"In the fall of 1905 I found a cycad in the Upper Cretaceous of Texas. The locality was 3 miles north and 1½ miles west of the station called Paloma, on the Eagle Pass branch of the Southern Pacific Railroad, and about 20 miles south of Spofford. At this place the Upson Clay is exposed on the east side of Sauz Creek, which joins with Cow Creek to form Elm Creek a half mile to the south. The exposure runs for a quarter mile north and south and is considerably cut up by gullies. At the north end the clay was dark and it contained a *Radiolites*, a small *Ostrea*, an *Anomia*, and *Exogyra ponderosa*. This last shell is frequent over the whole exposure. Eight fragments of presumably the same silicified trunk were noted. Three of these matched by their fractures and showed a stem about 10 inches wide, flattened considerably, and hollow. These three and one more fragment were all that I could carry, and they have been turned over to a specialist for study.

"The clay containing these fossils has been called by Dumble the Upson clay. (Augustana Library Publications, No. 6, p. 68. Rock Island, Ill.) It is from 500 to 600 feet thick in this vicinity and the stratum of this particular exposure is included somewhere in the upper 150 feet of the formation. Some sandstone ledges appearing 1½ miles south contain *Ostrea* larva and impressions of *Halymenites*, and these ledges mark the beginning of the change to the overlying San Miguel beds. This trunk comes from at least 1,400 feet above the base of the Upper Cretaceous in this State. The Upson Clay is underlain by about 750 feet of limestone of the age of the Austin Chalk, and below this there are here some 250 feet of sediments corresponding to the Eagle Ford shales. So far as I am aware, this is the only known cycad yet found in the Upper Cretaceous of America."

As yet, only the portions of armor from the single trunk constituting the type have been found. They indicate a rather infrequent form of preservation in which only the extraxylic or cortical and armorial portions of the trunk were silicified—the inner portions mainly failing of final conservation, probably with an early crushing out of the pith, resulting in a much flattened armorial sheath only. A very similar armor sheath from the Albien of the Argonnes, France, is figured by Fliche as *Cycadeoidea Colleti*. The latter specimen is said to consist mainly of iron oxide, though it does not appear to lack structure entirely, and as nearly as can be made out from the heliotype figure some young axial fruits are present. *C. Uddeni*, as very deservedly named in honor of its discoverer, who so carefully determined and recorded its stratigraphic position, presents features of very distinct interest. Although

in the absence of any dark staining the tissue differentiation is not well marked, the larger features are clearly indicated and despite a rough and checked light-colored flinty outer surface the fossil is one of very distinct beauty, as seen in all transverse polished surfaces from the outer armor and shown in the illustrations, Plate 3, photographs 1 to 3. In the sections the narrow zone of ramentum between the leaf and peduncle bases appears as a highly colored jaspery silica, while the leaf-base cavities are in large part filled, or perhaps the originally silicified leaf bases are partially replaced, by calcite (with some iron carbonate?). Further in towards the leaf-base insertions and in the cortical regions the structure is dense and the cut or fractured surfaces are nearly black. The checked outer surface of the armor, much like that of the Isle of Portland specimens, quite obscures the leaf-base spirals and does not reveal the presence of more than a very few of the numerous peduncles. But the sections show all the spirals and peduncles to a nicety. In these one at once notes in from a fourth to a third of all the frond axils the presence of rather slender peduncles of a very characteristic flattened isosceles triangular transverse section with the long side always nethermost. About midway out in the armor the peduncles give origin to two bracts, always laterally placed, and a little further out to a third arising from the superior side. At the periphery of the armor the bracts are still few, and several bases of fruits may be made out, showing conclusively that this cycad was characterized by rather long and slender peduncles bearing extra-armorial fruits enveloped by few, though relatively large, bracts. The general form and arrangement of the peduncles and bracts thus distinctly recalls that of the Boulder, Colorado, cycad, *Cycadeoidea nigra*, which may be specifically related, though plainly a differing species.

Only a single fertile series is indicated, and unless much reduced these numerous, more or less pendent flowers must have given the plant a most ornate appearance as it for the first time reached full bloom about the time of its fossilization. No evidence of branching is present; but the pauciform ramentum (a single cell in thickness) and the rather slender and long peduncles are fully in accord with our ideas of reduction and evolution in the Cycadeoideæ. It is much to be hoped that we may learn more of the flowers of the late Mesozoic representatives of the group.

It remains to add that in assigning the present form to a new species, despite an already overgrown list of petrified species, we may have regard not alone to the great time gap between it and the next older relatives of the Albien, but also to the likelihood of floral reductions and to the actual difference in form and dimension of the combined leaf bases and peduncle patterns. Such differences, though slight, and in a measure defying finality of comparison because of inconstancy in preservation of the outlines of the once living plants, as well as much variation in robustness of growth, appear clearly to justify a "new species," to say nothing of the greater convenience in cataloguing and handling a trunk widely separated from others in both latitude and time and deriving much of its interest by reason of this very fact.

Dr. Udden, in an extended paper on the geology of the region in which this cycad was found, shows its occurrence in the upper part of the 500 feet of clays called the Upson Clay, the characteristic accompanying fossil being *Exogyra ponderosa* and *Ostrea* larva, the latter only in certain sandy layers. The locality and horizon of *C. Uddeni* are hence accurately known and the prospect of securing more specimens is good.[1]

[1] Report on a Geological Survey of the Lands belonging to the New York and Texas Land Co., Ltd., in the Upper Rio Grande Embayment in Texas; by Johann August Udden. No. 6 of Library Publications of Augustana College, pp. 53–102, with 7 plates and map (Rock Island, Ill., 1907).

CHAPTER X.

NOTABLE EUROPEAN SILICIFIED CYCADEOIDS.

A fairly concise list of old-world Cycadeoids, citing original descriptions, horizons, and the museums in which the types are conserved, is given in Volume I (pp. 18–20). After the lapse of eight years, and after having had the opportunity of seeing nearly all of the original European types, it is not found that for present purposes this list requires material revision. It appears that the most serious omission is the fine group of semi-silicified casts described by Fliche (91) from the Albien greensand of the Argonne, in an important memoir on the Fossil Flora of that region which was wholly overlooked. These Argonne Cycadeoids are found at Clermont, Islottes, Revigny, and the Ardennes, and are of especial interest as representing, along with the Texas *Cycadeoidea Uddeni* of the Upson shale, the most recent occurrences known. The specimens include: (1) a Williamsonian stem with unusually large leaf scars, *Yatesia Guillaumoti;* (2) three typical Cycadeoidean stems of medium-size, *Cycadeoidea Argonnensis, C. Colleti; C. semiglobosa;* and (3) two Cycadeoid cones named *Amphibennetites Bleicheri* and *A. Renaulti.* This interesting group is accompanied by *Pseudo-Araucaria, Araucaria, Pinus, Cedrus,* and *Abietites* cones, besides coniferous wood, the cone series exhibiting some remarkably handsome types of conservation.

The Argonne Cycadeoids exhibit little change from earlier forms and retain a copious, well-conserved ramentum. The cones have their seeds fairly conserved for semi-casts, the dicotyledonous embryos being clearly outlined. The *Amphibennetites Renaulti* seeds are 11 mm. in length and 4 to 5 mm. in breadth, being the largest Cycadeoid seeds yet observed. The seed stems are very short, and only four to five interseminal scales surround each seed, this being a rather low number if really characteristic for the cones. Even so, there is some question if a new generic name is necessary, considering the variety of Black Hills cones illustrated in Volume I, some of which have the short stems and may at maturity have been large-seeded. So far, the mature seeds of the largest *Cycadeoidea* cones have not been observed with certainty.

Fliche goes on to call attention to a fossil seed from the Lower Cretaceous near Lewes, figured by Mantell as *Carpolithes Smithiæ,* which is very similar to the Argonne seeds, and he suggests that paleontologists may often have failed to recognize isolated Cycadeoid seeds (*cf.* 91, p. 55).

It is perhaps worth while to call attention to the fact that the *Cycadeoidea pictaviensis* (which is the *Bolbopodium* of Saporta, or form with the persistent disjointed leaf bases of varying length similar to the Isle of Wight *Fittonia squamata*) is from Montamise, not Montanaise, of the Upper Oxfordian near Poitiers. Renault errs in the spelling. The locality has been pointed out to me by Professor Jules Welch, of the University of Poitiers. The *Fittonia insignis* Saporta is also from the environs of Poitiers (Carriere du Grand-Pont).

A trunk not mentioned in the list of Volume I, because the original description was not at once obtainable, though cited in the references, is the very finely silicified specimen described by Raciborski in 1892 as *Cycadeoidea Niedzwiedskii* (226). The type is elliptiform, 30 cm. high, 25 cm. in diameter, and from an unrecorded locality in the Galician Carpathians. The horizon suggested by Raciborski is the Lower Cretaceous *Hornsteinschichten,*

which may also have yielded the great Dresden stem *Cycadeoidea Reichenbachiana.* These two specimens taken together render it not improbable that there is as yet hidden, somewhere in the Carpathians, a great mid-continental locality like the Black Hills Cycadeoid region. The Cracow trunk in quite every respect is a finely conserved lesser form which may be contrasted with the Dresden trunk, exactly as the small Wyoming Cycadellas compare with the larger trunks of the Black Hills series.

Of trunks mentioned in the previous list, one of the most important, which received no further comment, is the *Cycadeoidea* or *Clathropodium sarlatense* from near Sarlat in Dordogne (Paris Museum, Catalogue No. 1635). This is a beautifully silicified trunk of unusual intrinsic interest because it combines characters of *Cycadeoidea* proper and the Williamsonias. The heavy armor incloses a fairly thick wood zone with a rather smaller pith than in any other well-armored form. The specimen is a segment of a columnar trunk with a long diameter of 17 cm. and a short diameter of 12 cm. All the structure zones may be measured with exactness on the transverse surface. The pith has a long and short diameter of 22 and 9 mm., indicating an original diameter of only 1.5 cm. in the mid-region of the trunk. The wood is 1 cm. thick or over and the leaf bases from 4 to 5 cm. long, no lateral fruits appearing. The trunk is in a way distinct from all others known, and even if young may be regarded as ancestral to the bulky *Cycadeoideas* of late Jurassic and Cretaceous time. No closer study of this trunk has been made, but drawings and descriptions appear to indicate the presence of from 4 to 6 more or less discontinuous growth rings. The cortex is very thin. In a word, such a trunk may really fill the position of a true hypothetic stage between the more typical Williamsonians with small stems and the bizarre heavy-stemmed *Cycadeoideas* which seem to reach a maximum size as Cretaceous time begins. At least it is obvious that with some very slight change in any of the trunk regions, such as an exaggerated tendency to retain wilted leaf bases, transformation scarcely involving the woody cylinder at all might result in medullar and cortical thickening leading up to the most robust forms. For on last analysis there may be a relatively slight structural hiatus between some Williamsonian with a stem no thicker than a lead pencil and the huge spherical type like that illustrated on Plate 14, and it is absolutely certain that the Triassic forms like *Wielandiella* were the more cosmopolitan, if not truly ancestral.

Of new trunks described since Volume I was published, there is but a single example, a small subspherical specimen, also from Dordogne (Limeyrac), described by Lignier (155) in 1910 as *Cycadeoidea Fabre-Tonnerrei.* This fossil, like the American *Cycadeoidea mirabilis,* is of a yellowish or jaspery aspect, like "gun-flint," and the horizon to which it belongs is likewise indefinitely placed as either Jurassic or Cretaceous. In fact, the chief difference between the globose Dordogne specimen and the Colorado trunk is the more columnar habitus of the latter.

In giving additional notes on European Cycadeoids it is not especially necessary to take up formally the four important Isle of Portland species *Cycadeoidea megalophylla, C. microphylla, C. portlandica,* and *C. gigantea.* This is rather a subject for English students, although, as earlier explained, the Portland quarries have been operated so long that a fine representation of trunks, including some of the most striking forms, has gradually made its way into the U. S. National and Yale Museums. As the checked, rugose appearance of the Portland Cycadeoids makes it exceedingly difficult for one unfamiliar with such specimens to readily judge the actual interest of a given trunk, the various collections are of more or less equal importance; and the two American series certainly afford quite all the material and much of the data needed for critical comparisons. The cylindrical core

sections illustrated in figure 39 by no means represent the best that can be had from the English material at hand; but they are obviously more characteristic than any sections hitherto figured, and particularly in certain areas of these sections the preservation of the ramental mass between the leaf bases is of peculiar clearness and beauty. The all-important point in the investigation of these specimens, which paleobotanists seem to have neglected, is the necessity for selecting large areas for study, preservation being very unequal. Taken as a whole the preservation is poor; but with patience one critical feature after another is found most excellently conserved. As in the case of the American trunks, and as has already been emphasized, several genera may actually be present, although it is greatly to be hoped that neither English nor any other students will disturb the already generically

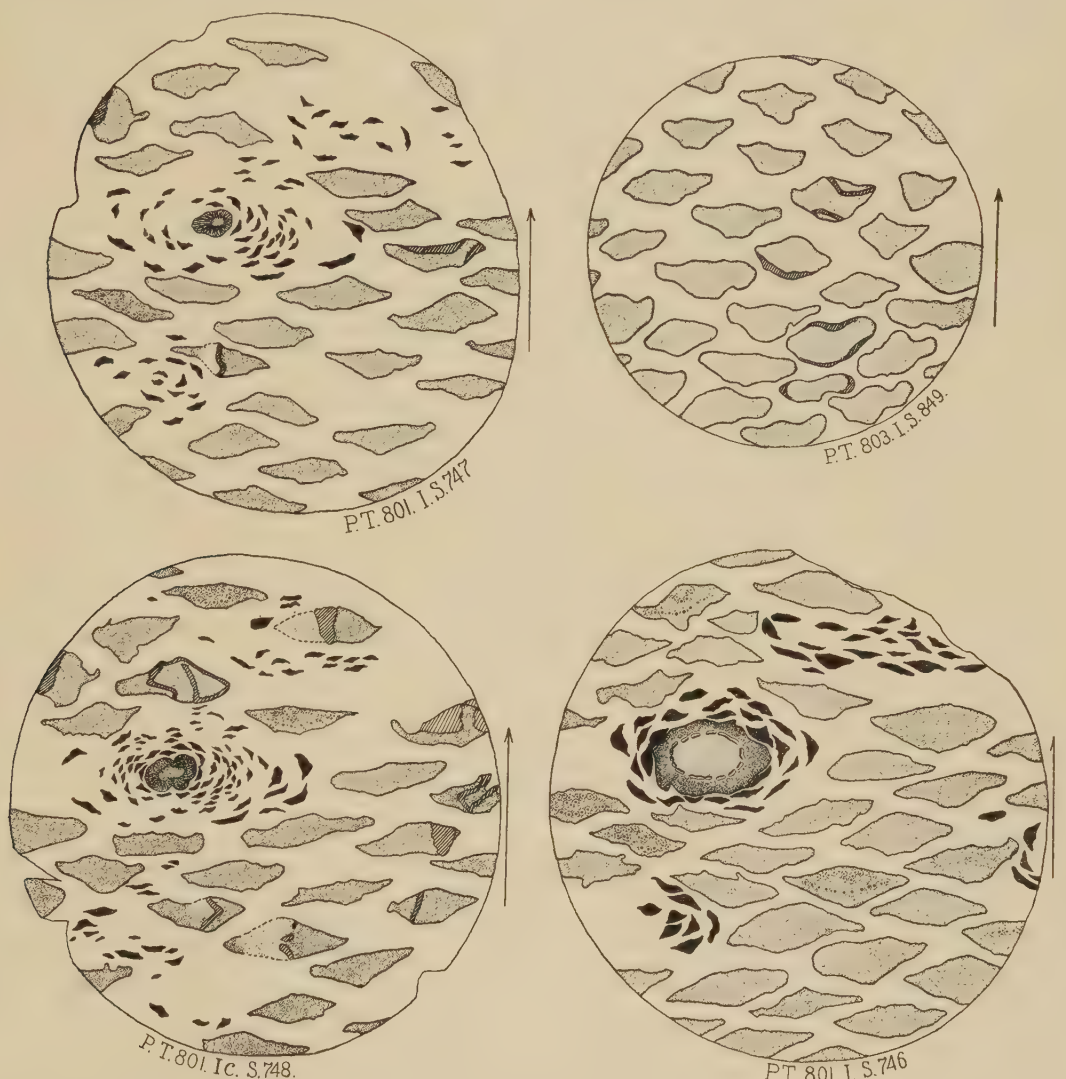


FIG. 39.—*Cycadeoidea* (*Bennettites*) *microphylla* or *portlandica*. Three serial transverse core sections from the Isle of Portland, trunk No. 801 of the Yale collection, and one such section from trunk No. 803. All four sections are shown natural size.

The three core sections 746, 748, and 747 show structures specifically comparable to the similar armor sections of American trunks. They indicate a considerable abundance of young fruits, either undeveloped or ovulate; while in trunk 803 (section 849) the leaf-base spirals are as yet undisturbed by fruit growth. It is probable that the trunks from which these sections were cut, together with the so-called type *Bennettites portlandicus*, to which provisional reference might be made, are true examples of *Cycadeoidea microphylla* Buckland.

overburdened literature of the Cycadeoids without the most careful consideration; and it is above all things desirable that those generic definitions which are gradually developed may be possible to apply in the determination of new material. As the case stands to-day, there is much more of scientific judgment and credit in the avoidance of new generic definitions than there is likely to be in their attempted establishment. The silicified Cycadeoids have become such a great and important group that the simplification of their nomenclature is of more present interest and value than new species or new genera founded before the old and the long-known forms have been far more thoroughly studied than now.

Aside from the Isle of Portland series the European specimens which possess the greatest interest in all comparisons with the American series at the present time are unquestionably (1) *Bennettites Gibsonianus*, (2) *Fittonia squamata*, (3) *Cycadeoidea Reichenbachiana*, and (4) *Cycadeoidea etrusca*. To these our attention may now be more formally turned.

Bennettites Gibsonianus Carruthers.

1870. *Bennettites Gibsonianus*, Carruthers. On Fossil Cycadean Stems from the Secondary Rocks of Britain. Trans. Linn. Soc. London, pp. 694–698, Pls. 58–60.
1890. *Bennettites Gibsonianus*, Solms-Laubach. Ueber die Fructification von Bennettites Gibsonianus, Carr. Botanische Zeitung, Vol. XLVIII, Leipzig, col. 789–798; 805–816; 821–833; 843–847; Pls. IX, X. Translated in Annals of Botany, Vol. V, London, Nov. 1891, pp. 419–454, Pls. XXV, XXVI.
1892. *Cycadeoidea+Bennettites Gibsonianus*, Capellini e Solms-Laubach. I tronchi di Bennettitee dei Musei Italiani. Notizie storiche, geologiche, botaniche. Mem. d. R. Accad. delle Sc. dell'Ist. di Bologna, Series V, Vol. II, Bologna, pp. 161–215, Pls. I–V.
1894. *Bennettites Gibsonianus*, Lignier. Végétaux fossiles de Normandie. Structure et Affinités du Bennettites Morierei Sap. & Mar. (sp.). Mémoires della Soc. Linnéenne de Normandie, Vol. XVIII, pp. 5–78, Pls. I–VI, Caen.
1894. *Cycadeoidea (Bennettites) Gibsoni*, Ward. Proc. Biol. Soc. Washington, p. 79.
1900. *Bennettites Gibsonianus*, Scott. Studies in Fossil Botany, pp. 447–472.
1899. *Cycadeoidea (Bennettites) Gibsoni*, Wieland. Am. Jour. Sci., Vol. VII, pp. 383–391.
1906. *Bennettites Gibsonianus*, Wieland. American Fossil Cycads (numerous references).
1911. *Bennettites Gibsonianus*, Wieland. Am. Jour. Sci., Vol. XXXII, pp. 133–155, Figs. 2A, 2B, showing seed coats of original type.
1915. *Bennettites Gibsonianus*, Stopes. Brit. Mus. Cat. Cretaceous Plants, Part II, pp. 23–47.

No description of American fossil cycads can be considered quite complete without a definite and formal reference to the Isle of Wight type *Bennettites Gibsonianus*. Its description in 1870 with the discovery of the ovulate cones marks one of the milestones in the investigation of fossil plants and since that time references to this notable Cycadeoidean have been so numerous that the bounds of an ordinary synonymy have long since been passed, it only being feasible to cite the contributions which have directly added to the description and study of the original type.

According to the very latest results of fossil cycad study, there is no sufficient structural difference, no single feature or group of features, definitely separating *Bennettites* as a distinct genus of the Cycadeoideæ. It is certain that the species *Bennettites Saxbyanus*, with *B. Peachianus* and *B. portlandicus*, should logically be placed in the genus *Cycadeoidea*. There is, therefore, no very urgent need for retaining the genus *Bennettites;* and this fact is given expression in the above synonymy. But in view of the further fact that the references to the Isle of Wight type as *Bennettites Gibsonianus* are so numerous in paleobotanic texts, it seems better to avoid, at least for a time longer, the formal transference to the genus *Cycadeoidea*. Consequently the name *Bennettites Gibsonianus* is used throughout this work more or less in contravention of those ordinary rules of nomenclature the valid application of which would require inclusion in the genus *Cycadeoidea*.

It is not necessary to give a detailed description of the Isle of Wight type in the present connection. In the first place, the original description of Carruthers, so far as it goes, is

an excellent one, and subsequently the more necessary extensions were given by Solms in his paper on the fructification, including the discovery of the dicotyledonous embryos (1890); while my own studies of the seed coats, based on sections prepared from the original type material, have at least confirmed if they have not slightly extended the descriptions of Solms.

In fact, while a more searching and extended study of the wood zone and the apical region, such as has hardly been carried out in the case of any fossil cycad, could be made with more or less profit, almost the only larger trunk region remaining relatively unstudied is the thick cortex or cortical parenchyma as traversed by the leaf-base and peduncle traces. But it may be safely assumed that the cortex has the characters seen in *C. Wielandi;* nor do any of the sections from any part of the trunk show other than strictly typical *Cycadeoidea* structure. Of this I am certain, since, through the exceeding kindness of Capellini, I have been enabled to base all my notes on characteristic sections cut from a wedge of the original type, and can also give a few further figures of very considerable interest in addition to those of testal features which are more conveniently inserted in the chapter on seed structures.

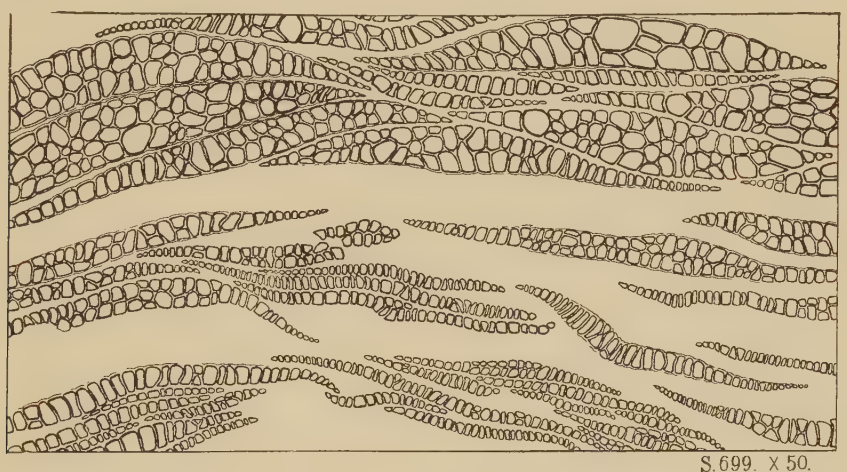


FIG. 40.—*Bennettites Gibsonianus* (section cut from original type). ×50.

Characteristic transverse section through ramentum from lateral region of trunk between old leaf bases and fruits with mature seeds. Inspection of the figure shows the characteristic thickness of the scales to be three cells of the average size, the scales tending to be a trifle broader than those shown in Vol. I, Fig. 18, under the name *Cycadella ramentosa*. Compare also with the ramentum surrounding a young leaf shown on Pl. XVIII, Vol. I. These two ramental types do not differ appreciably from each other.

The ramentum (*cf.* Fig. 40) is of the large-celled form observed especially in the Wyoming cycads, reaching three or four cells in thickness. The wood structure is further illustrated by the photomicrographs of Plates 33–36, showing the close agreement with various American types, particularly *Cycadeoidea Wielandi.* From this latter form the wood is hardly distinguishable, except for differences in appearance due solely to conservation. As in *C. Wielandi,* there is some wood parenchyma, and the main body of wood is composed of scalariform tracheids.

The photomicrographs reveal very clearly the remarkably distinct type of preservation which distinguishes *Bennettites Gibsonianus* from almost all other cycads, leaving it, in this respect at least, in a class quite by itself. The sections lend themselves unusually well to photography, the cell contents being clear and the cell walls especially dense. The fossil is not nearly so quartzitic as in most American specimens. The main mass, as determined from sections from the type, is an opalaceous or hydrous quartz, the cell walls

having as their chief coloring substance, or even their chief constituent, FeO and Fe_2O_3, with, perchance, some magnetite in places. Calcite may be present on the outside of the leaf bases, but has not been definitely observed. The preservation somewhat obscures the wood cell scalariform markings, but one may easily see that the mass of the wood is characteristically scalariform throughout, with the exception of any spiral primary wood and a thin zone of pitted (?) cells next the cambium. This same distribution of rather lightly scalariform secondary wood is found in many American specimens.

Since the foregoing paragraphs were written, Stopes's (1915) British Museum Catalogue of the Cretaceous Flora, Part II, has appeared. A number of pages are devoted to *Bennettites*. Figures of a seed base (p. 39) and of the xylem and phloem structure are added to the illustrations already extant. Instead, however, of going on and comparing the structure of *Bennettites Gibsonianus* type with that of Isle of Portland specimens of *Cycadeoidea megalophylla* and *C. microphylla*, Dr. Stopes ignores *C. megalophylla*, perforce the primary type of the genus *Cycadeoidea*, transfers Carruthers's *Yatesia Morrisii* to *Cycadeoidea*, and then attempts to show that *Cycadeoidea microphylla* was polyxylic.

Now, it is unfortunate that English conservators have not kept track of the original Buckland types. It has been known for some years that these types could not be found for study, although the excellent figures of Buckland make it quite certain that they must sooner or later be found. However, it is not indispensable to find these types. The validity of the genus *Cycadeoidea* does not depend on them alone. The two species *C. megalophylla* and *C. microphylla* are well represented in the Portland "dirt bed," and specimens of both are to be found in both the American and the European collections. The writer has cut sections, as elsewhere noted in this volume, from both types of trunks. *Cycadeoidea megalophylla*, which Dr. Stopes would so arbitrarily dismiss in order to make a place for the microphyllous form, is characteristically monoxylic. The woody cylinder is fairly well conserved and agrees structurally with that of *Bennettites Gibsonianus*, the main body of secondary wood being lightly scalariform, with a thin zone of pitted tracheids next to the cambium. The only observable differences from the Isle of Wight specimen are specific rather than generic and, as contended earlier in this volume, fail utterly to pass family boundaries. The *C. microphylla* is also monoxylic as the first fruits appear.

On turning to the *Cycadeoidea microphylla* secondarily entitled to represent the genus *Cycadeoidea*, it is clear that the figures are not quite so convincing as desirable. Buckland gives, aside from the smaller leaf bases, the main distinction as follows:

> "The trunk is longer in proportion to its width, whilst its transverse section exhibits at the centre the same indistinctly cellular appearance as the species last described; but near the circumference instead of one it has two laminated circles, and exterior to each of these a narrow band devoid of laminæ, analogous to the two bands of cellular substance that are placed in similar relation to the two laminated circles in a recent Cycas. These two circles, like the one circle of *Cycadeoidea megalophylla*, approach the circumference, whilst those in Zamia and Cycas are placed nearer the centre of the stem."

Commenting on this statement Dr. Stopes says:

> "It is curious that this important and interesting feature in the anatomy of the type of *Cycadeoidea* has been overlooked by writers who discuss the nomenclature of the Cycadophyta as though *Bennettites* and *Cycadeoidea* were identical. In Buckland's figure of the external features of *Cycadeoidea microphylla* there is no sign of cones among the leaf-bases, and there is nothing to show that its fructification resembled that of *Bennettites* in any particular."

The point involved here depends on the single specimen which Buckland says was all that he saw, and it appears that the supposed bicambial cylinder analogous to that of

Cycas was inferred from the apical transverse section, which is inconclusive and the only one figured. Other writers have not lain stress on this point, because lesser trunks of *Cycas* are monoxylic, and strengthening of the woody cylinder may be, probably is, little more than a specific character in *Cycadeoidea*. Some of the species of the latter form, with a relatively thin woody cylinder comparable to that of *Bennettites*, were monocarpic, while in the case of forms with a heavy woody cylinder there is less evidence of monocarpy and the trunk may have reached a greater age. Evidently strengthening of the woody cylinder which Stopes finds in various columnar trunks, probably Williamsonian rather than Cycadeoidean, whether polycambial or monocambial in nature, is largely a matter of greater age. The trunk sections determining the time of the first appearance of the young fruits in the armor of *Cycadeoidea microphylla* have never been cut, so that the absence of recognizable indications of bract areoles or peduncles in Buckland's figure is absolutely without significance. Frequently, too, in American trunks the presence of young fruits is not obvious on the armor surface. Had the trunk been a larger one, either fruits or peduncles would have been seen. The fact can not be too strongly emphasized that *Cycadeoidea*, far more than *Cycas*, was a cosmopolitan and diversified genus which, mainly owing to its peculiar features, left behind a surprising array of fossil representatives; and exactly because of this fact, as well as for the sake of a nice regard for priority, it becomes both convenient and necessary to make *Cycadeoidea* and not *Bennettites* the more elastic generic term. Under the circumstances it is more necessary to accumulate the data of trunk structure than at once to attempt to define sharply the limits of the various genera composing the Cycadeoideæ. Only by so doing may a very burdensome synonymy be avoided. (See page 92.)

Fittonia squamata Carruthers, 1870.

1847. *Clathraria anomala* (in part), Mantell. Isle of Wight, p. 295.
1854. *Clathraria Lyellii*, Mantell. Isle of Wight, 3d ed., p. 217.
1870. *Fittonia squamata*, Carruthers. Trans. Linn. Soc., Vol. XXVI, p. 690.

The type and only ascribed example of Carruthers's genus *Fittonia* is a remarkably handsome cast in the Jermyn Street Museum of Practical Geology, London; but if memory serves there is in the Paris Museum a very similar specimen of much the same size and appearance in every respect, from Montamise near Poitiers. This is consistently called by Saporta *Cycadeoidea pictaviensis*.

Carruthers characterizes *Fittonia* as a short obovate trunk with slender woody axis enlarging upwards, and a large cortical layer, the *scales* and bases of the petioles being large, imbricated, at first reflexed, then ascending. Specific features are oblong scales with an obtusely rounded apex, petiole bases contracted near the insertion, with a V bundle pattern and a phyllotaxy of 8/21. The type is thus further described:

"The bases of the petioles are few in number in proportion to the scales, and occur irregularly among them, though both organs are arranged in the same series. Neither fruit nor foliage has been found associated with this fossil, but from its striking affinity in those characters, in which it can be compared with the South-African *Encephalartos*, I can not hesitate in placing it with *Yatesia*, near that genus.

"The only specimen hitherto found of this fossil is a singularly perfect cast of the stem. The cavity originally occupied by it has been filled with the amorphous substance of the rock in which it was buried; and the cast thus made is so perfect that the external markings of the scales and petioles and the impressions of the vascular bundles are exhibited; while each scale, though closely adpressed to its neighbours, is yet free from them even at its base. The original organism must have been incrusted with a crystallized mineral, like calcite, which, after the decay of the vegetable tissues, received and moulded the amorphous matter of the cast. This mineral has been redissolved and carried away, so that what remains is a remarkable facsimile of the original, as far as the outer surface is concerned."

There is, of course, nothing in the foregoing description to prevent the inclusion of the Isle of Wight cast in the genus *Cycadeoidea*, which, in fact, is even demanded by the V-grouping of the petiolar bundles; but there is no more thankless task than the renaming of historical specimens, even though both defensible and demanded. The strictly comparable *Cycadeoidea* casts described by Fliche from the Albien-Cénomanien of the Argonne (91) afford further interesting examples of cast preservation of cycad trunks, it being quite curious that thus far no similar casts have been found complementing the great American series of silicified Cycadeoids.

FIG. 41.—*Fittonia squamata* Carruthers. Trunk cast from the chalk-marl of the Undercliff near Ventnor (Bonchurch), Isle of Wight. × ⅓. From Carruthers (51).

Hitherto the interpellation of scale leaves in the regular and unbroken foliar spirals would, of course, have been regarded as a distinctly Cycadacean feature; but this character is now definitely determined in such forms as *Cycadeoidea ingens*, *C. Jenneyana* and *C. Dartoni* (*cf.* Figs. 9, 10, 12, and Plates 10–12). As now well established, the distribution of leaves and scales in alternating nodes is the constantly recurring feature in *Williamsonia*. The rather slight development of ramentum in *Fittonia* may, moreover, be somewhat dependent on the mode of preservation. In every respect, therefore, the Isle of Wight *Fittonia* suggests characters that are at once intermediate between the two great groups of Cycadeoids, and yet affords, as Carruthers was quick to see, resemblances to *Encephalartos*. It is quite possible, too, that just such a form may have borne its *Williamsonia*-like fructifications more nearly apically than other Cycadeoids.

The original specimen, Mantell says, is 15 inches in length by 11.5 inches in width. Such a specimen uncrushed would have a greatest diameter of perhaps 8 inches. There is some uncertainty as to the exact source of this cast. Mantell speaks of it as having been discovered in the chalk marl of the Undercliff by Captain Ibbetson, near Ventnor, on the south coast (west of Bonchurch). But Carruthers says that Etheridge held the mineralization and matrix character to indicate as the source of the specimen the Wealden at Brook,

so prolific in silicified logs. The *Cycadites Saxbyana* (Robert Brown, 1851), in Morris' Catalogue of British Fossils transferred to *Cycadeoidea*, is from the Wealden of Brook Point. Casts or cast-like forms should theoretically occur with the silicified stems, but such association has never been reported authentically. The American trunks most nearly resembling *Fittonia* are the whitish, usually much crushed, silicified "Cycadellas" of the Freeze Out Hills.

Cycadeoidea Reichenbachiana (Göppert) Capellini et Solms.

1755. Hippuriten oder versteinerte Corallenbecher, Eilenburg. Kürzer Entwurf der Königlichen Naturalienkammer zu Dresden, p. 24.
1771. Vegetabilische Versteinerung, Walch. Die Naturgeschichte der Versteinerung zur Erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur, Pt. III, p. 150; Atlas, Supplement, Pl. III*a*, Fig. 6.
1844. *Raumeria Reichenbachiana*. Göppert. In Wimmer, Flora von Schlesien, ed. II, Vol. II, p. 217 (nomen).
1853. *Raumeria Reichenbachiana* (Göppert). Jubiläums-Denkschrift d. Schles. Ges. f. vat. Cult., p. 262, Pl. VIII, Figs. 4–7, Pl. IX.
1887. *Raumeria Reichenbachiana*, Solms. Fossil Botany (Trans., 1891), pp. 99, 100.
1892. *Cycadeoidea Reichenbachinaa* (Göppert), Capellini et Solms. Mem. Real Accad. Sci. Ist. Bologna, Ser. V, Tom. II, p. 188.
1894. *Cycadeoidea Reichenbachiana*, Ward. Proc. Biol. Soc. Washington, Vol. IX, p. 85.
1899. *Cycadeoidea Reichenbachiana*, Ward. Ann. Rep. U. S. Geol. Surv., XIX, 1897–1898, pp. 601, 604, Pl. LIX.
1904. *Cycadeoidea Reichenbachiana*, Ward. Am. Jour. Sci., Vol. XVIII, July, pp. 40–52, 1 fig.
1906. *Cycadeoidea Reichenbachiana*, Wieland. American Fossil Cycads, Vol. I, pp. 13, 33.
1908. *Cycadeoidea Reichenbachiana*, Wieland. Am. Jour. Sci., Vol. XXV, Feb., pp. 95–97.
1911. *Raumeria = Cycadeoidea Reichenbachiana*, Schuster. Sitzungsber. K. Bayerischen Ak. d. Wiss. Math.-phys. Kl. Hft. III, pp. 489–499, Text-figs. 1–4, Pls. I, II, III, Figs. 1–6.

At once the finest conserved and one of the two or three most famous of all European fossil cycads, the great type of the Zwinger Museum at Dresden, *Cycadeoidea Reichenbachiana* affords a notable comparison with the Black Hills trunks. Collected about 1753 or earlier, it has been owing to a mere scientific mishap that this historic specimen failed to afford the starting point in the discovery of fructification in the family and group to which it belongs; and it must always remain a curious speculation as to just what impetus an early study of the Zwinger trunk, appearing perchance about 1870, when Carruthers and Williamson made their notable contributions, if not 40 years earlier at the time of Buckland's and Brown's discovery of the Cycadeoideæ, would actually have given the subject of paleobotany, always a little late in the development of its more severely scientific phases. However, the mistaken ardor which at times leads conservators of fossils to regard as a sort of "Barbarei," disengagement from the matrix, or sectioning requisite to ultimate study, is confined neither to cycads nor to any one country.

Perhaps in the present instance, owing to the bonanza-like richness of the Black Hills *Cycadeoidea* localities, a time may come when the sectioning of the Dresden trunk can yield no further store of fact than a few lesser specific details, a time when, as a more or less superficially studied but absolutely well-founded type, it should have a double significance to the museum visitor for whose benefit it is kept intact and unseen. Professor Ward has given, in his most interesting history of this "famous fossil cycad," far too long to record here, a letter from Count Solms-Laubach referring to the unwillingness of the Zwinger curators to have their sole stem cut. And I may add that subsequently to the publication of Volume I of these studies I received a further letter from Count Solms explaining that after the completion of his investigation of the Italian Cycadeoideas he had not only offered to personally superintend the cutting at the works in the Fichtelgebirge, but to bear the considerable expense involved. How grandly this careful and adequate study by the famous Strasburg paleobotanist would have added to the interest, visible beauty, and scientific value of the Zwinger type it is quite needless to descant upon. The action of the Dresden custodians is, of course, explicable on certain grounds, though the

exact opposite of that of Capellini in bringing within the range of scientific knowledge the Italian cycads, including especially that other historic European specimen, *Cycadeoidea etrusca* (*q. v.*). It is obvious enough that with the progress of discovery the function of the museum normally changes and the display of the "wonders of nature" becomes more and more subsidiary to a more adequate emphasis of the philosophic value and the economic necessity of increasing as rapidly as possible the world's store of accomplishment and proven fact.

Description of the macroscopic features of *C. Reichenbachiana* other than has already been given by Göppert (1853) and Ward (1904) is unnecessary here, the principal details of interest being supplied by the accompanying text-figures. As Professor Ward says, there is a rather closer resemblance to the Black Hills *Cycadeoidea Jenneyana* than to any other form, except that the bract-enveloped floral axes are far more conspicuous, their great size suggesting the larger flowers of the branching trunks from Minnekahta.

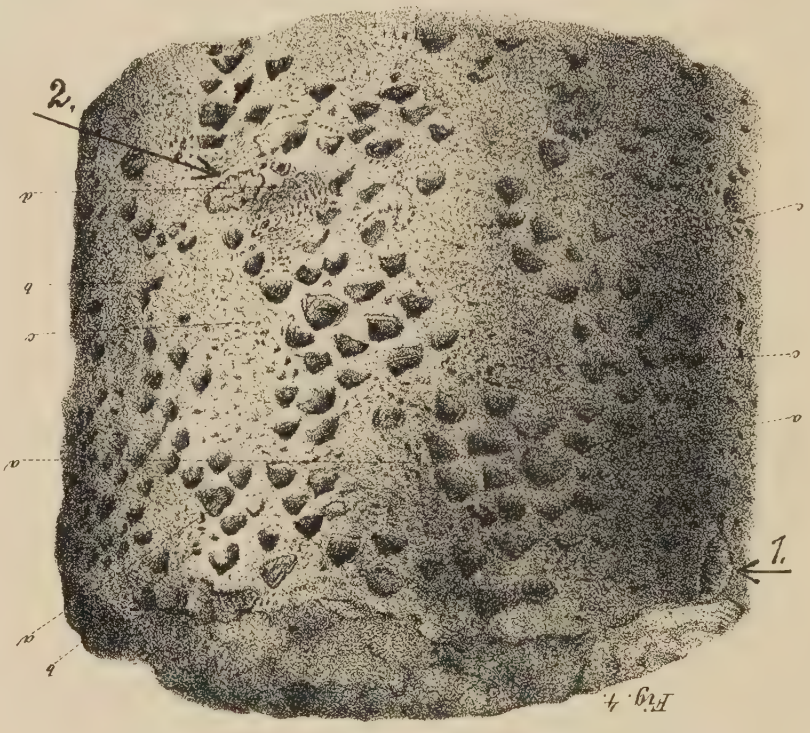


FIG. 42.—*Cycadeoidea Reichenbachiana.* Original figure from Göppert's Tab. VIII. Oriented with retention of original lettering. The added arrows indicate the large fruit scar (1) and the staminate disk of 16 microsporophylls (2).

The inverted position in which this figure appears in Göppert's plate may have been brought about by the rather variable leaf-scar shading, although the drawing is an otherwise excellent one. In Figure 43 the trunk is rotated about 30° to the right, and the disk with its microsporophyll scars and heaped synangia comes sharply into view.

The texture of the trunk is like that of the finest preserved and least chalcedonized trunks from the Black Hills localities, conservation throughout being exceedingly good. On inspecting this type myself, on the occasion of a visit to Dresden early in July 1907, I found it somewhat difficult to determine the exact limits of the wood zone, owing to the dark colors that so often go with fine conservation, so that Professor Ward's measurements may stand for the present, being approximately correct. He gives for the medullar diameter 13 cm., with a thickness of about 8 cm. for the woody cylinder, the very heavy armor ranging from 5 cm. to a normal thickness of about 10 cm. These measurements are, of course, basal and show that the specimen is a nearly true basal segment of a markedly columnar trunk. The woody cylinder, though thick as compared with *Cycadeoidea etrusca*, *Bennettites Gibsonianus*, some of the Isle of Portland specimens, and many American forms, is far exceeded in size by *Cycadeoidea ingens* and several undetermined trunks of columnar habitus from Black Hawk (*cf.* Plate 4). There is some flattening, the long diameter being 52 cm. and the short diameter 10 cm. less. A longitudinal section on the short diameter would be the best.

By far the most important feature I was able to observe was the presence of finely conserved bisporangiate strobili with disks of 16 microsporophylls. (See Figs. 42 to 44.) This was such a wholly unexpected and interesting discovery that the notes then made and published a year later (386) may well be repeated here, as follows:

"*Cycadeoidea Reichenbachiana* * * * consists in the basal segment of an immense silicified cycad trunk a full half-meter in diameter and of noticeably but not markedly compressed unbranched columnar form. In life it may have been more than a meter high, as the segment recovered is over a half-meter in height and without tapering.

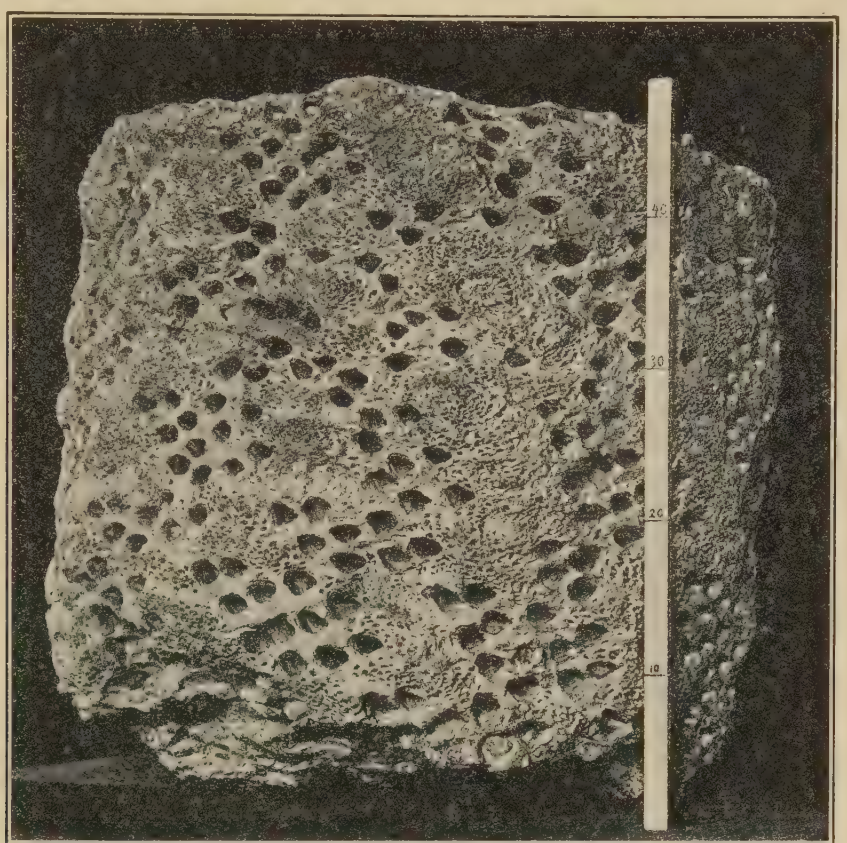


FIG. 43.—*Cycadeoidea Reichenbachiana.* Photograph of type showing numerous bract areoles and staminate disk denoted by arrow 2 of figure 42. $\times \frac{1}{5}$. From Schuster.

"The leaf-bases are a little smaller than those of *C. Jenneyana* and *C. ingens*, and of much the same size as those of *C. gigantea* of Seward from the Isle of Portland, and the very similar *C. excelsa* of Ward from the Black Hills. The trunk has just emerged from its pulcherrima stage of growth, that pre-fructification period well illustrated by *Cycadeoidea megalophylla* Buckland; and, as indicated by large groups of bracts marking the individual axes of fructification, and especially by the manner in which the bracts close in compactly at the center of the bract groups, many young fruits are present. Of these fruits three, and perhaps more, are very clearly in the bisporangiate or non-dehiscent-disk or flower-bud stage so well exhibited by our American specimens. Moreover, in one of these three buds the disk structure is strikingly clear. In it the curved middle portions of the unexpanded and presumably bipinnate microsporophylls have been so eroded away as to clearly reveal in transverse section sixteen circularly disposed microsporophyll rachides. And one may plainly see that these sections of the rachides of triangular outline abut and enclose an inner mass of closely packed and wonderfully conserved synangia of large size, rising above and concealing a central ovulate cone. The individual synangia are evidently attached to the rachides in normal position. This is the first time that the presence of such silicified flowers has been definitely confirmed in European trunks.

"In size and general structure the bisporangiate strobilus of *C. Reichenbachiana* with its 16 microsporophylls closely agrees with that of *C. dacotensis* with 17 or 18, with perhaps a decidedly interesting difference in the apparently larger size of the synangia. The structure of the synangia is unquestionably preserved; indeed, although familiar with quite 1,000 trunks, I know of no other fossil cycad so beautifully and magnificently silicified as *C. Reichenbachiana.* It is even probable that the entire structure of the staminate fronds as well as the synangia is preserved in the greatest perfection, whence it is of very distinct interest to paleobotanists that, as I was informed at Dresden, Solms-Laubach is soon to carry out an exhaustive histologic study of this famous fossil cycad.

"Göppert supposed these axes to be vegetative and like the lateral buds of old *Cycas* stems; but Professor Ward notes that they are fruits and thought seeds must be found in some. In which he is wholly correct, since nearly all must bear young ovulate cones hidden beneath the thick husk of enclosing bracts, which is in the great majority of cases all that can be seen at the surface of the trunk. Fully fifty young floral axes are present."

It appears that both of Göppert's figures of *Cycadeoidea Reichenbachiana* may have been inverted during the course of publication and that both author and artist possibly intended to depict their wonderful petrefaction in its normal upright position. Indeed, Professor Nathorst has in a letter called attention to an altered annotation in the earlier and later author's copies. The evidence for such an explanation is not quite apparent in Göppert's figure 4, here reproduced with the retention of the inverted lettering as figure 42; but a more careful inspection of the large inverted armor area engraved in about the natural size on Göppert's Tab. IX reveals the fact that the specimen must have been viewed in the normal position. The leaf-base shading, as well as that of the fruit or fruit scar at the lower edge of the plate, conforms to a left lighting. But the drawing can also be explained as one made from the inverted position with a right illumination. However this may be, the fruit scar at the lower edge of the specimen denoted by the arrow (1) of Figure 42 is not happily interpreted. The outlines suggest a central cushion cavity surrounded by a mass of radiating seed stems and interseminal scales as in *Cycadeoidea dacotensis*, or in any large *Williamsonia*-like strobilus; and one might even imagine that features from some other specimen were introduced. The *Denkschrift*, however, mentions only one other small trunk, the *Raumeria Schulziana*, and there is no evidence that the Dresden trunk was ever subjected to summary methods of study during or since the time of Göppert.

While, therefore, an ovulate fruit of much the character so imperfectly shown was doubtless present in life, it appears that the artist merely reversed his shading of the curved bract impressions, and so failed to indicate as a concavity the deep scar left by either a shed or an imperfectly conserved fruit. The defects are, in short, such as are characteristic of most illustrations of fossils, especially plants, previous to the extended use of photography; and that this drawing is quite inexact was likewise observed by Professor Ward. Nevertheless, careful scanning of Göppert's figures, taken point by point, shows that the artist saw and carefully depicted the bisporangiate strobilus indicated by the added arrow No. 2, figure 42. In a drawing of this size the flower bud could scarcely be more clearly shown, and it is very interesting to observe that had author and artist made this flower the subject of their chief illustration its extraordinary character could by no possibility have escaped their attention. Just what accidental circumstance led Göppert and his artist to confine their attention to a strobilar cavity and sketch that imperfectly, instead of studying and illustrating with painstaking care the most remarkable of all fruits from the Mesozoic rocks which they held in hand, may never be known. Fortune sometimes smiles on the investigator, but is ever and anon most ironical. Here, therefore, as in many other instances of the illustration of historic fossils, the wonder is not so much that the artist drew so

poorly, with such curiously varying ability and success, but rather that he could not be a little more discriminating in the representation of crucial features, and in places, albeit, a little less painstaking in the attention given to unessential details. For it has rarely happened that treatises on fossils have been overillustrated, and these illustrations are certainly among the most deeply interesting sketches of fossils studied as "petrifactions," rather than as forms with wonderfully conserved histologic structures from which may be deciphered the history of ancient plants. Just one hundred years before the publication of Göppert's excellent work, Knorr and Walch had indeed figured an armor portion of *Cycadeoidea Reichenbachiana* as clearly as such trunk features are shown in this volume. But immediately following this figure appears a drawing of one of the so-called "Megara stones" without scientific significance.

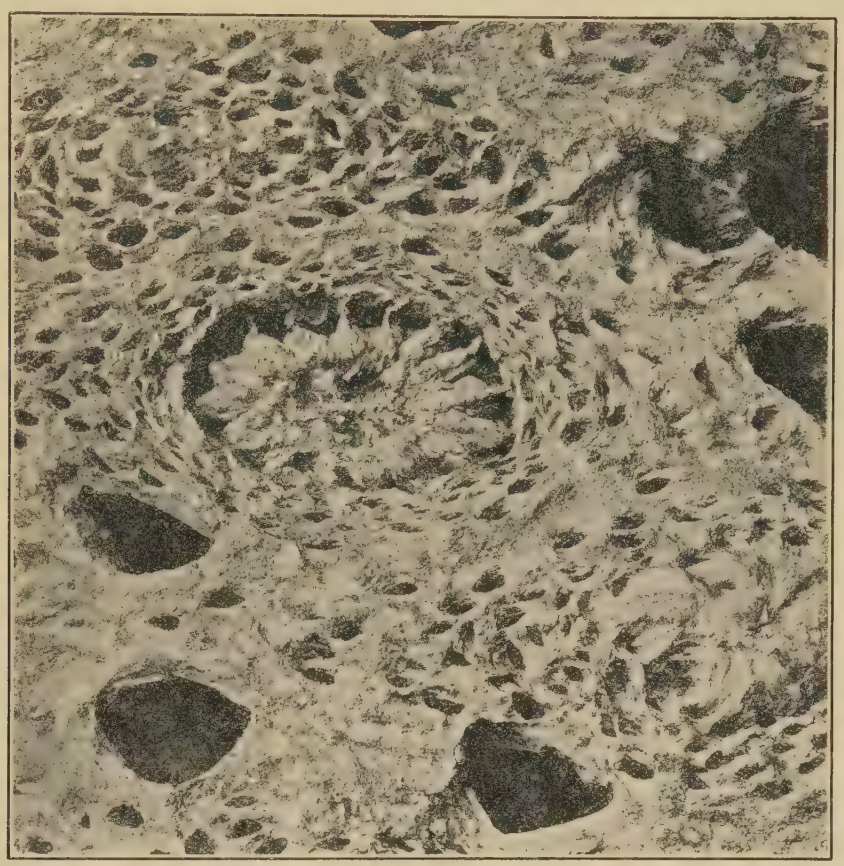


FIG. 44.—*Cycadeoidea Reichenbachiana.* Partly eroded staminate disk indicated by arrow 2, Fig. 42. Natural size. This disk of 16 microsporophylls is one of three or four borne by the great Dresden type which remains unstudied. From Schuster.

The only further structural feature of *Cycadeoidea Reichenbachiana* which at present remains to record is that the thin sections of small size made from spawls from the wood zone (synonymy, 1911) have precisely the same type of secondary wood, cambium, and phloem as *Bennettites Gibsonianus*, *Cycadeoidea etrusca*, *C. megalophylla*, and various Black Hills trunks. Any differences in these several forms are so inconspicuous that on the basis of such small isolated sections, or those from approximately the same trunk region, specific variations are hardly discernible.

Nearly as conclusively as any other form known to me, the large area of the armor of *Cycadeoidea Reichenbachiana* occupied by fruits suggests a monocarpic habit of fructification, while the fact that only about three of the fifty axes present still retain their staminate disks, though none of the ovulate cones reach any considerable size, must indicate primarily either a bisexual condition, which is the more probable, or diœcism. But it is also true that an adequate series of fruit sections, such a series as could be obtained by sectioning all the fruits from that one-fourth of the trunk which contains the plainly conserved disk, might show considerable difference in ovulate development and even indicate a partly bisexual and partly monœcious habitus. If when a final study is made much variation in ovulate development is found present, care should be taken to secure, as far as practicable, true median sections of the cones in order that their relative development may be clearly brought out. Inasmuch as the Black Hawk columnar trunk No. 115 of the Yale collection, Plate 6, photograph 2, must be regarded as definitely monœcious, while in the *Cycadeoidea dacotensis* trunk No. 214 of the Yale collection, from which a large proportion of the axes were cut and illustrated in Volume I, the evidence obtained is less conclusive, it would be deeply interesting to know whether or not the functionally bisexual condition is definitely indicated in the famous trunk of the Zwinger Museum.

Cycadeoidea Etrusca Capellini et Solms.

1892. Capellini and Solms-Laubach. Mem. Real Accad. Sci. Ist. di Bologna, Ser. V, Tom. II, pp. 177, 181, 204, 212, 214, 215, Pl. I, Fig. 2; Pl. IV, Fig. 1; Pl. V, Figs. 7, 8.
1899. Wieland. Am. Jour. Sci., Vol. VII, p. 389, Figs. 17–20.
1906. Wieland. American Fossil Cycads, Vol. I, pp. 5, 12, 33, 139–141 (bisporangiate strobilus), 167, 159 (pollen figured).
1908. Wieland. Am. Jour. Sci., Vol. XXV, pp. 94–95.
1909. Scott. Fossil Botany, p. 579.
1909. Capellini. Mem. Accad. Sci. Ist. di Bologna, Serie VI, Tomo VI, Pl. I, Fig. 6.

The famous Etruscan cycad of the Capellini Museum at Bologna has a treble distinction. From the position in which it was found on a tomb in the old Etruscan necropolis at Marzabotto, this handsome basal trunk segment of medium-sized columnar type was regarded with curiosity by the Etrusci more than 4,000 years ago; moreover, a symmetrically polished-out area on one side may even indicate an earlier Neolithic use as a sharpening stone. In a sense, therefore, this fossil has some claim to be regarded as having had the longest-known history of which there is any record in all the annals of paleontology. Secondly, it has the distinction of having yielded the first clue to the approximate position of the staminate fructification in the Cycadeoids through Count Solms's discovery of the pollen grains of one of the better conserved axes of fructification. Again, *Cycadeoidea etrusca* is an unassailably well-founded species, and there is exceedingly small probability that it is identical with any previously described form whatsoever, although a typical species of the Buckland genus *Cycadeoidea*. As such it has an especial interest as one of the forms with very small flowers. In the summer of 1907 I had the opportunity to study the original type and then made the following notes:

"The features of this segment of a columnar trunk are already familiar through the descriptions and figures of Capellini and Solms. The specimen is of great beauty, the texture dense, the color quite dark, the general outer appearance somewhat intermediate to the Wyoming *Cycadella* and *Cycadeoidea nigra* from Colorado. Numerous young fruits are present, and through the great courtesy of Senator Capellini I was enabled to study thin sections prepared from one of these some years since. Especially the thin section of the young axis figured by Solms is of even greater interest than I had anticipated; for although the tissues of the sporophyll rachides are mostly broken down,

the entire and uncompressed outlines of both the sporangia and the walls of the synangia of the usual *Cycadeoidea* (Marattiaceoid) form seen in the American specimens are certainly often present. Only the individual cells of the outer or palisade layer of the synangia do not seem to be conserved. An outline of a synangium cut in the longitudinal transverse direction is quite distinct; while an obliquely cut synangium shows three adjacent sporangia filled full of collapsed (or desiccated) pollen grains, the enclosing locular walls being very perfectly conserved. The pollen is seemingly mature and the synangia are even larger than in *C. dacotenis*, although the fruits are of a much smaller size.

"The small central ovulate cone, no more than a centimeter long, is very perfectly outlined, the short stalked and minute ovules are distinct. In size and general structure these fruits may eventually prove more like those of *Cycadella* than *C. dacotensis*. From the rather small size of the staminate fronds, it seems that these were more reduced than in *C. dacotensis* or *C. ingens;* but whether they were bipinnate, pinnate, or simply consisted in a single blade, bearing synangia laterally inserted, much as the megaspores are borne by the carpophylls of *Cycas*, remains impossible to say. These small fructifications may at least prove to have a rather more reduced form than those of *Cycadeoidea dacotensis*. Transverse sections of *C. etrusca* fruits are lacking, but should be made, as they may show the disk features much better than do longitudinal sections. The vegetative structures, however, agree with those of the Maryland cycads very closely throughout—only the species remaining fairly distinct from *Cycadeoidea marylandica*, if we hypothetically consider the plant on the basis of vegetative features alone.

"I may add that I also had the pleasure of visiting the wonderfully interesting and picturesque Etruscan town site and necropolis where *C. etrusca* was found. These ancient ruins are situated in the grounds of Count Aria in the picturesque valley of the Reno, 20 miles west of Bologna in the foot-hills of the Apennines. After seeing how the stream is there cutting away the last remnants of what was once a regularly laid out town of considerable size, I am still more impressed with the likelihood of the suggestion I have once made [Vol. I, p. 5] that not a few of the fossil cycad trunks were gathered into towns or cities now in ruins or long since destroyed. That *C. etrusca* is at least as ancient as the old River Reno Etruscan village and necropolis of 4,000 years ago is certain; for it bears near its base, as noted by Capellini, an elliptical polished-out depression of considerable size, due to use as a smoothing or a sharpening stone, which may just as well have been of neolithic as later date. At any rate, the great perfection of the specimen indicates that in all probability it did not occur alone; and perchance the occurence of associated silicified conifers may yet aid in giving some clue to the original locality, which, if found, would doubtless yield other cycad specimens of rare perfection and interest."

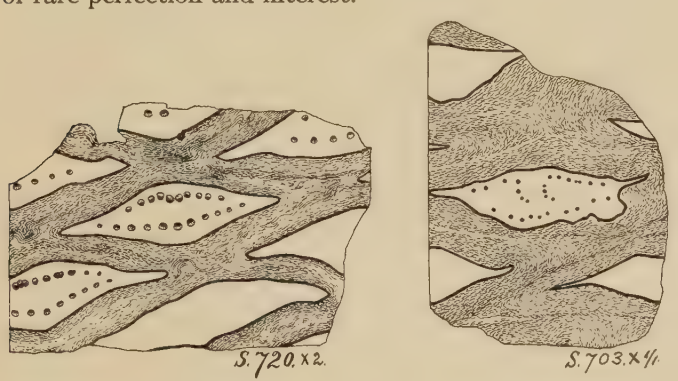


FIG. 45.—*Cycadeoidea intermedia* and *Cycadeoidea etrusca* transverse armor sections compared. The *C. intermedia* section 720 is enlarged twice; the *C. etrusca* section 703 is natural size.

In their leaf-base, size and form, bundle development, and bundle pattern, these two species from the scaly clays of Italy differ markedly from each other and are distinct. The *C. intermedia* is noteworthy for the large size of its leaf-base bundles, which have their phloem region strongly invested by heavy-walled tissue. In both forms the ramentum is regularly one cell thick, but the *C. etrusca* investment has more than twice the development of that of *C. intermedia*.

Subsequent to this preliminary study of the type at Bologna, Capellini forwarded to the Yale Museum a symmetrically cut wedge from which a series of sections illustrating the vegetative features was prepared. These sections show very nearly the same type of wood zone as *Cycadeoidea Wielandi* and *Bennettites Gibsonianus*. As in both these species and the Wyoming cycadeoids of the Freeze Out Hills, the wood is almost entirely composed of finely scalariform tracheids and the cortex is moderately thick. The leaf-bases are of an intermediate size with characteristic bundles (*cf.* text-figure 45, and Plate 30, phot. 5).

The ramentum is abundant, but fine-haired. The conservation of the vegetative structures is exceedingly good, although owing to density of texture, apparently due to more or less carbonaceous material in the cell walls, the sections require to be made unusually thin to bring out the structural details in their full clearness. It might eventually prove desirable to study one or two more of the fruits; but in the case of so unique a specimen it would seem that for once sentiment might be permitted to play a part wisely and prevent any further cutting of this most curious memento of a civilization as old at least as that which chiseled out its code in the black diorite of Hammurabi.

CHAPTER XI.

THE SEEDS OF CYCADEOIDEA.*

The lore of fossil seeds is of very recent date. It may be fairly said to begin with the sections of the English "coal-ball" seed *Trigonocarpon*, cut and figured by Hooker and Binney in 1855. Twenty years later came the important studies by Williamson, who named and described various of the calcified seeds so richly represented in the English "coal balls." But he scarcely produced any single work on seeds that may be compared with the superb monograph on the much scantier French material: "Les Graines Fossiles Silicifiées," which constitutes the last great work of Brongniart (1881).

Indeed, it is almost entirely within the past score of years that a sufficient body of work has been accumulated to bring the fossil seed structures into the range of critical study, and even yet the number of contributors remains very small, mainly because no wholly new sources of material have been discovered since the time of Williamson and Brongniart. As will be remembered, Carruthers' study of the seeds of *Bennettites* (1870) and Williamson's restoration of *Zamia gigas* appeared simultaneously. The material for the study of petrified seeds being, with the exception of purely modern types of Tertiary or comparatively recent formations, so exclusively confined to the English coal balls (those of Austria never having been adequately studied), present-day contributors on fossil seeds are mostly English. The progress made may be briefly told.

In France Bertrand has given critiques of the earlier work of Brongniart, and Renault and Grand Eury have written on *Cordaites* and *Rhabdocarpus*. In England Oliver and Scott (1904) have studied minutely the several species of *Lagenostoma* in an epoch-making contribution, proving that these seeds were borne by *Lyginodendron*. Though David White actually observed seeds attached to the foliage of *Aneimites* quite as early as Oliver and Scott made their discovery, his paper, which also appeared in 1904, was long in press. Oliver and Salisbury (1911) have published an admirable account of the seeds of the *Conostoma* group—this being, in fact, one of the most critical of the structural studies yet published. Oliver alone has given the restoration of the singularly handsome seed *Physostoma* (1909), and a more recent critical and most elaborate study of the striking type *Trigonocarpus shorensis* is by Salisbury (1914). Professor (Miss) Benson has given a fine reconstruction of the cupule-inclosed *Sphærostoma*. Mrs. Arber (Miss Agnes Robertson) has completed the picture of the platyspermic *Mitrospermum* (1910). Following Hooker and Binney (1855) and George Wild (1900) on *Trigonocarpus*, Scott and Maslen have studied *Trigonocarpus Parkinsoni*, and *T. Oliveri* (1907); also Miss Prankerd (1912) has added a study of *Lagenostoma ovoides*. Briefer papers which should be mentioned are those of McLean (1912) on the prothalli of *Bothrodendron* and *Lagenostoma*, and especially that of Miss Berridge (1911) on *Gnetum gnemon*, establishing a certain parallel with *Cycadeoidea*. Also Mrs. Thoday (Sykes) has given a suggestive comparison of the *Gnetum* and Bennettitalean seeds (1911).

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*The study of the *Cycadeoidea* seeds is here taken up as a separate topic of wide interest. An increasing specific series invites extended comparison with other gymospermous seeds, and the possibility of some direct analogy between seed coats and floral envelopes requires discussion. A special and essentially complete chronologic list of the contributions on fossil seeds is appended to this chapter. References are by years.

Meanwhile, Newell-Arber (1905) has described from impressions new species of *Lagenostoma*, showing most interesting details of the manner in which such seeds were borne and the very prolific character of some of the pteridosperms. Nathorst has very recently added descriptions of casts of Paleozoic seeds in the light of all this larger knowledge of their structure (1914), and Bertrand (1913), using Nathorst's chemical methods for study of carbonized impressions, has brought to light curious characters and as yet very little understood features of cycadofilicalean fructification, suggesting pointedly enough that the study of ancient seeds is only fairly begun. Such a general fact was, of course, already inferred from the strong resemblance to seeds of the remarkable microspore-bearing disk *Codonotheca* of Sellards (1903).

Standing remote from the seeds of Paleozoic time, those of *Cycadeoidea* alone among Mesozoic gymnosperms have afforded an interesting basis of comparison with ancient and to a certain extent also modern forms. More profusely represented than any other fossil seed whatsoever, the *Cycadeoidea* seeds have proven a fertile field of study and will long so continue. To the original notes of Carruthers have been added the fairly critical studies of Solms-Laubach (1890), Lignier (1894), and Wieland (1911). But it is obvious that several years more must elapse before all the facts can be clearly gleaned from the rich store of material already at hand.

That an adequate interpretation of testal and other seed structures forms one of the central problems of botany taken in its broadest sense has been clearly recognized. As Oliver has well said, "the evolution of the seed was one of the most pregnant new departures ever inaugurated by plants." Nor has the scantiness of material just noted, the hard and stern limitation to a bare score of well-known forms of all the tens of thousands of ancient seeds that must have existed in past time, deterred the students of seeds from making the most of the meager fossil record thus far brought to light. Indeed, the study of existing seeds has been no more assiduous, and many a parallel with the fossil forms yet remains to be drawn. Not only so, but now that it has been shown that if the disks of *Cycadeoidea* were to become sterile the prefoliate form would mimic the complex seed coats seen in the older gymnosperms, a new interest is added. As will be explained later on in the present chapter, some kind of dual homology between seed and flower is certainly suggested; and it is not too much to say that with this discovery the entire subject of fossil seeds has taken on a greatly increased fascination and interest.

In the preliminary volume on the fossil cycads it was especially pointed out that continued study of the seeds promised much of biologic interest. It was, of course, recognized that far more careful treatment of the American forms was required, together with a comparison of European forms. The present chapter on seeds is, therefore, merely the logical continuation of what has gone before. It is held to be far better to thus present the more critical details of seed anatomy in a body than to treat them separately in connection with species. So doing will even serve to accentuate rather than obscure some very excellent specific indices afforded by the cycad seeds.

AMERICAN AND EUROPEAN CYCADEOID SEED MATERIAL.

As just remarked, the best-known old seed types are chiefly gymnospermous and Paleozoic, with the notable exception of the Mesozoic Cycadeoideas. But, fortunately, whatever the latter lack by reason of isolation they more than make up by abundance and exquisite preservation in half a dozen different species. Not only is the structural representation ample, but the number of mature strobili now runs into the thousands. In fact,

the subject of Cycadeoidean seeds has assumed a continuous interest. For, in addition to the mature seeds, we have the seeds well outlined in many young strobili varying in size all the way from a pea to a small pear, as well as a proembryonic stage, considered present in one form (*Cycadeoidea McBridei* ? Y. S. 131), while the fully developed dicotyledonous embryos are finely conserved and have now been seen by thousands!

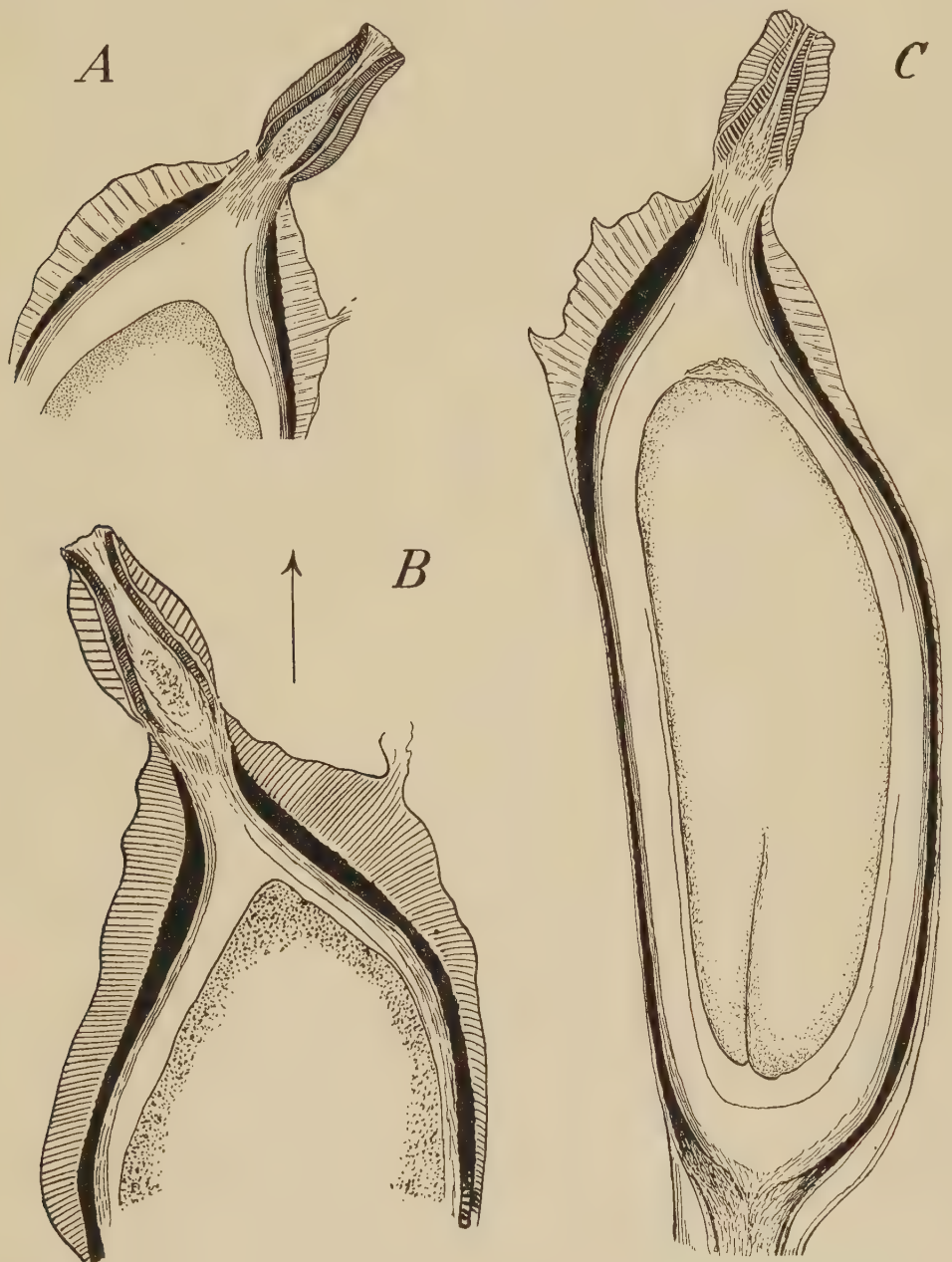


FIG. 46.—*Cycadeoidea Dartoni.* Longitudinal seed sections. A, C, ×40; B, ×50. A, drawn by Weber; B, C, by Wieland.

In each instance a large embryo is present. The so-called "tent-pole" region appears to be indicated in many of the seeds and a plinth-lagenostome, denoted by a thin black line in each of the drawings, may be present, the connection between some such line and the nucellar apex being indeterminate. These three drawings are sufficient to show the ribbed character of the pentamerous seeds; the stone (in solid black) has a double thickness on the rib line, while the palisaded "blow-off" is somewhat sculptured. The figures are purposely given in large size as a basis for further study and pencil notes.

Of single trunks which have added much to our knowledge of seed characters and fruit habits in the Cycadeoideæ a considerable number might be mentioned; but that trunk which easily surpasses all others in striking features and richness in conclusive details is the specimen found by Dr. Darton, of the U. S. Geological Survey, and described elsewhere in this volume as the type of the new species *Cycadeoidea Dartoni*.

Even as illustrated by Professors Coulter and Chamberlain in their textbook on the Morphology of Gymnosperms, in only a single small text-figure this specimen shows something of its extraordinary characters, while, on inspecting the original, one can have but the single first thought—that the fossil record can become rich indeed! On plotting the lateral surface of the Hermosa specimen it became evident that even the half trunk as collected bears from 500 to 600 ovulate cones, thus exceeding all records in fossil plants. Of these cones, not all are in equally complete conservation. In the course of erosion from the containing beds, one side of the trunk has suffered some loss of fruits. The other side is in perfect conservation all the way to the apex of the trunk, which is fortunately complete and made up of a heavy mass of hairy bracts, among which not a trace of young pinnules has been observed. (See Plate 42, photograph 4, and Plate 43.) The life of the trunk, it seems, must surely have come to an end with the maturation of its heavy series of fruits.

For initial study a lime-coated armor portion of hand-specimen size was broken away from the base of the trunk in the full certainty that it must also contain the abundant fruits deeply hidden in the concealing and protecting ramentum. None the less, the surpassing beauty of the sections obtained was scarcely anticipated. The first section cut (the transverse one, Plate 49, phot. 1) revealed a superabundance of fruits, the bract groups

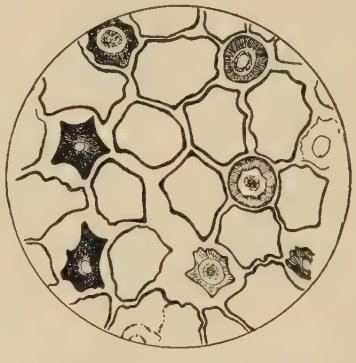


FIG. 47.—*Cycadeoidea dacotensis*. Portion of section illustrated on Plate 20, phot. 2, showing extreme tips of micropylar tubes surrounded by interseminal scale heads. ×20.

These seeds are very young and small, it being most interesting to find the pentamerous ribbing with traces of pentad minor ribs more accentuated than in later stages of growth and continuing nearly to the extreme end of the tube, which is rounded. Exclusive of the cupule the transverse section of the *Gnetum africanum* tube is similarly pentamerous. Observe that to the right the extreme end of the micropylar tube is seen, while the darker sections to the left pass a little lower down at the point of greatest constriction.

being rather small, and the leaf bases even slightly shrunken. The entire armor was thus found packed with strobili to an extent that could not have been fully anticipated. Even in this first lesser section there were revealed three entire and two nearly entire axillary ovulate strobili, with but two of the five complementary leaf bases. With the cones thus located, an armor section was at once cut through the summits of three adjacent ovulate cones. (*Cf.* Plates 42 and 45.) Subsequently large and approximately tandem tangential sections were cut in a virtually complete series passing from the initial section nearly to the small and at last slightly scattered fruits at the base of the bract-surmounted trunk apex. These are illustrated in the series of Plates 41 to 50, which may serve to show the remarkable character and richness of fructification in *Cycadeoidea Dartoni*.

In all the cones the mineralization is after the manner of silicification, not so distinct as calcification, but yet excellent; and nearly every seed contains a mature embryo, not so well conserved as those of Yale trunk 131 (illustrated in Volume I, Plate XXII), although showing quite satisfactorily the character of the embryonic tissues. Especially valuable for

purposes of comparison are these embryos, because little desiccated or otherwise shrunken, and with the epidermal cells nearly always more or less distinct. Other sections of *Cycadeoidea* embryos showing more detail are abundant, but none are more beautiful than these.

In the course of the elaboration of material for this volume, moreover, many new strobili of various trunks have been studied. Also, in addition to those cut from the Black Hills trunks, I have made seed sections from a trunk wedge of *Bennettites Gibsonianus* of the Isle of Wight, and already had at hand the sections of *Bennettites Morierei*, obtained from Professor Lignier, as related in Volume I. In short, there has been brought together a representation of all the forms so far known, except, of course, the lost Buckland specimen illustrated on Plate 63 of the Bridgewater Treatise; and on the basis of this complete representation it is now thought feasible to go far toward rendering the paleobotanic text

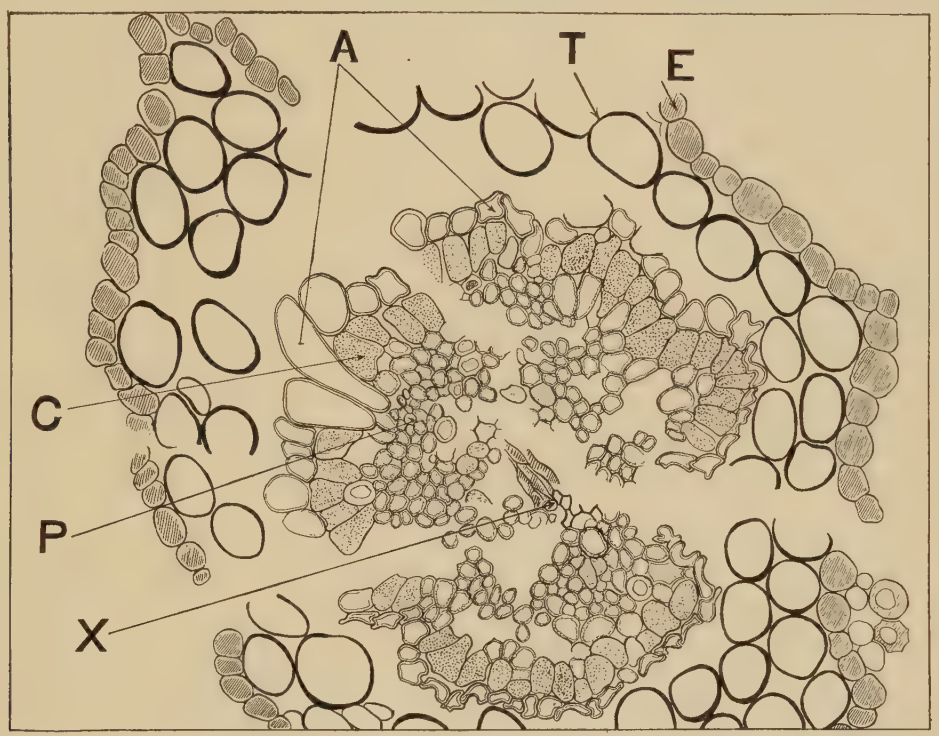


FIG. 48.—*Bennettites Morierei* type (Sap. et Mar.). × 100.

Transverse section of seed stem traversing point of greatest constriction exactly where expansion into the hilo-chalazal region begins. (Camera lucida drawing from a section cut by Professor Lignier.)

X, xylem or central tracheid region surrounded by stem ground-tissue; P, small-celled outer ground-tissue; C, stained layer ="*assize colorée;*" A, imbricate to pleated layer ="*assize plisée;*" T, tubular cells of cortical region forming exterior of seed stem, and basal husk of seed; E, outer woody layer of the 5 to 6 enveloping interseminal scales.

on the Cycadeoid seeds short and satisfactory; although to say even approximately the last word will, of course, not be possible. For one thing, with the superb and unequaled material already at hand, it may at all times be expected that to-morrow will yield better cut or more fortunately conserved seeds of any of the species; and such surely will, from time to time, make possible those accurate drawings of transverse and longitudinal seed sections which it was hoped might be given here in the case of some forms. But it can be readily understood that in the course of past section-making there have been some failures of technique in getting the very best sections from the material—some disappointments. It is easy to grind away those small micropylar tubes (!) and the aim should consequently be to avoid more and more any loss of material through impatience or lack of skill on the part of the sector.

PREVIOUS DESCRIPTIONS OF TESTAL FEATURES.

As is always inevitable in the case of a complex fossil plant structure, the different types of mineralization, in this instance nature's own variation of her staining and embedding methods (!), result in slightly different interpretations in the hands of different investigators. What with this factor and different modes of illustration or study of areas and features seldom taken from the same region of a seed, or showing variation of a given region in one and the same seed, it becomes all too easy to suspect greater differences in even a small group of species than actually exist, while meantime certain salient features are likewise easily overlooked. So it has proven in the case of the cycads, though of simple enough structure on closer study. In order, consequently, to bring out a fundamentally clear comparison of all the seeds, American as well as European, showing the best testal conservation, camera-lucida drawings have been made of longitudinal sections at a point about one-third of the distance from the base to the tip, as reproduced in Figure 49. Before taking up these, however, it is desirable to briefly recall the several interpretations of the *Cycadeoidea* testa.

According to Carruthers' original study of 1870:

> "In *Bennettites Gibsonianus* . . . Two envelopes inclose the albumen and embryo. The outer envelope or testa consists of a thin layer of delicate elongated cells; the inner is composed of a single layer of oblong cells arranged with the longest diameter at right angles to the walls, and indurated by a considerable amount of secondary deposits. . . . two coverings were produced upwards into a tubular exostome or styliform process . . . spread out like a stigma in the upper surface of the pericarp."

In this description and illustration of the general features of the seed the first or inner layer of collapsed fleshy cells immediately beneath the indurated layer is not mentioned, Carruthers then going on to say that—

> "Inclosed by these envelopes is the nucleus with its membranous covering and abundant albumen . . . the subrectangular cells of which are obvious in several seeds. . . . The albumen was solid behind the embryo, but was divided from top to bottom down its center, in front of the embryo."

Here we have unmistakably clear allusion to embryonic features and tissue; for the supposedly albuminous "subrectangular cells" are simply the cotyledonary epidermis and mesophyll, uniform in appearance and peculiarities of preservation, in the embryos of *Bennettites Gibsonianus*, *B. Morierei* and several American specimens, all known in satisfactory detail.

In the next description of these cycad seeds, that of Solms-Laubach (1890), the embryos were clearly recognized, and the testal structure accurately described as follows:

> "Three distinct testal regions are to be noted, a basal, middle, and apical. In the middle region of the seed the testa is closely appressed to the nuclear membrane, and wherever well conserved three distinct layers may be recognized, the middle layer of which is simply a single stratum of short, prismatic, palisaded, thick-walled, dark-brown cells; while the inner and outer layers consist in several thicknesses of rather small thin-walled tissue. The tissue of the inner layer is mostly crushed and indistinct, while that of the outer layer appears as a light area following the palisade layer, and finally passes over into more or less distinctly confluent growth with the walls of the seed cavity. At least a distinct boundary appears but discontinuously. . . .
>
> "In the apical region of the seed the testal layers were found most difficult to delimit, owing to a lack of sections traversing the long and slender micropylar tube in the true median longitudinal position and the large amount of pyrite investing the peripheral tissues of the strobilus in irregular areas."

In no form are the testal features conserved with more of diagrammatic clearness than in the French specimen *Bennetites Morierei*, Lignier's description of which soon followed that of Solms, as already mentioned. In fact, the seeds of this isolated strobilus are conserved in such unrivaled perfection as to leave nothing more to be desired except the

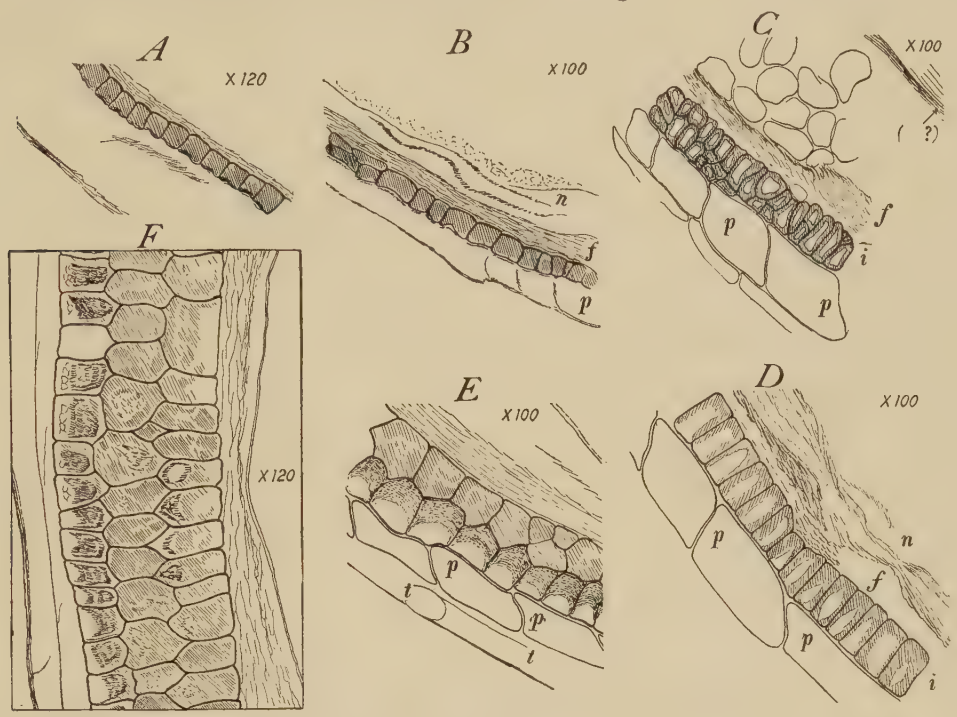


FIG. 49.—Longitudinal sections of Cycadeoidean testas at point two-fifths of the distance from base to apex, except F. ×100 to 120.

A. *Cycadeoidea* sp. (*not C. Wielandi*). Wealden equivalents (Lakota) of the Black Hills.

B. *Cycadeoidea Macbridei* (*?*), with thick blow-off layer very poorly conserved. The sclerenchyma layer of squarish cells with their inner basal wall heavy.

C, D. *Bennettites Gibsonianus* (type). Two seeds from one and the same cone of original type. Lower greensand. Isle of Wight.

E. *Bennettites Morierei* (Sap. et Mar.). The type from Oxfordian or more likely Lower Cretaceous (*cf.* Lignier) of Calvados, Normandy.

F. *Bennettites Morierei* (Sap. et Mar.) type. ×120. Longitudinal section of testa traversing valley below the shoulder, where ribs first become prominent. Note here, as in E, the *inner part* of the middle stone called by Lignier "*tissu charnu*." This is thin or absent in other forms.

i, indurated layer arising from C of fig. 48; *p*, the outer fleshy or "blow off" layer arising from A of fig. 1 and expanding into five or six alæ near apex, sometimes forming horns; *f*, collapsed tissue of inner flesh; *t*, tubular cells forming lax or frayed husk, whence these cells may or may not appear in the longitudinal section (=T, fig. 48); *n*, the nucellar-sack tissue, always quite susceptible to silicification.

Between the inner flesh (*f*) in various American seeds, and the nucellar sack (*n*), as well as in the seed of *Bennitites Gibsonianus*, often occur loosely compacted large cells, supposed to be nucellar contents (pre-embryonal tissues). In the initial course of silicification collapse of the inner flesh would favor rupture of the nucellar sack with more or less dispersion of such rounded cells, but this explanation is tentative. The close agreement of the two European species and the American forms retaining the "blow off" layer is noteworthy, while the two seeds of *Bennettites* showing difference in the indurated layer, as seen in about the same region of the testa, suggest the character of longitudinal fluting, and completely bridge the slight structural gap between the commoner American form and *Bennettites Morierei*, no more than mere specific differences appearing.

recovery of a second example, and make us anxiously ask if French collectors have really sought for further material in the original locality as diligently as they might. From the description of Lignier (1894), which enters into much detail, we need not, however, quote in full in the absence of a series of photomicrographs, though before passing on to the American seeds it should be mentioned that the limiting region between the seeds and surrounding scale-formed seed pit, which, as we have just seen, Solms found difficult to see in *B. Gibsonianus*, is always distinct in *B. Morierei*. In any of the sections from the latter one may

clearly see that the appearance, as of a peripheral confluent growth of the seed wall with the interseminal scales, is due to appression and the failure of the scales in places to develop their epidermal layer continuously. There thus arises a *pinching out* into a single ribbon-like layer of interseminal epidermis appressed closely to the very outermost cells of the seed. The condition does, however, show how, as the result of close growth and suppression of epidermal cells, a form of intergrowth could easily arise. Quite the only structural feature of the testal wall that Lignier leaves in doubt is the nature of the inner cells of the middle stone, whether stony, or, as he is inclined to believe, fleshy. On this point the American species throw some light, and to comparisons with them we may now turn.

COMPARISON OF TESTAL STRUCTURE IN AMERICAN AND EUROPEAN CYCADEOIDEAN SEEDS.*

On comparing the descriptions of the testa already quoted, namely, those of Carruthers (1870), Solms (1890), and Lignier (1894), with each other, and with those given for the American seeds by the writer, a most substantial agreement within strict generic limits will be found and the differences due to conservation will fully appear, if these two explanatory paragraphs be borne in mind:

(1) The comparative study of all the known *Cycadeoidea* seeds and a fairly extensive list of existing gymnosperm seeds shows that the middle layer of the seed wall is essentially a stony rather than a merely indurated or suberous layer, and much thicker in *Bennettites Morierei* than in any American species. Lignier's description of the inner cells of this layer as fleshy was given with some reservation, and it is merely necessary to note that the stony layer shows varying degrees of induration in allied species throughout the gymnospermous series.

(2) In referring to the writer's own descriptions of testal structure, as given in Volume I with too few figures, all stress must be laid upon the fact that the seed is there spoken of as it probably appeared on splitting loose—as a shed seed—and that the form primarily dealt with is *Cycadeoidea Wielandi*, which has only traces of ribbing and now proves to have the most reduced testal structure known, being almost, or wholly, without an outer fleshy or "blow off" layer. Better sections from cones of other species show well-marked ribbing and a heavy "blow off" to be commonly present in the Black Hills Cycads. But so far there is no instance in which this structure shows the fine detail in any silicified specimens that it always exhibits in the ferrized *Bennettites Morierei*. The middle or indurated zone appears to have been far more susceptible to preservation by silicification, whereas the outer or "blow off" layer of the seed is infinitely better stained and conserved by iron carbonate. Indeed no one who sees the original preparations can fail to be struck by this complementary reaction of the outer flesh and middle stone to these two types of mineralization, as seen in the Calvados strobilus and the Black Hills fruits.

This explanation, then, entirely clears the way to a complete understanding of the similarity of testal development in the American and European fossil cycads. The seeds of the Cycadeoideæ containing embryos vary from 1 cm. in length in *Amphibennettites Renaulti* of Fliche (1891) to 3 or 4 mm. in length in the smallest American forms, and there is a remarkable homogeneity in the testal features of the entire group. In fact, short of close study, the only differences discernible are in the ribbing and size of the seeds, with some variation in the thickness of the tissue zones of the seed wall, which is normally three-layered, with a distinct middle stone. The outer flesh alone may, however, exhibit, aside from pecu-

*In these comparisons the names of testal features and seed parts proposed by Oliver and Salisbury (1911) are employed, having been found convenient and usable, while a close reading of the present text will disclose one or two extensions of this necessary *nomenclature of use.*

liarities due to the unusual manner in which the seed is completely encased in the solid husk of interseminal scales, marked reduction or even elimination.

Of the several species *Bennettites Morierei* has distinctly the heaviest walls, *B. Gibsonianus* walls of intermediate thickness, and some of the American seeds the thinnest walls of all, though there is essential agreement in testal structure extending to the cell types of the three component layers. To show this structural similarity and to further bring out minor details proving that in *Cycadeoidea* we deal with a genus of world-wide distribution and long persistence in time, I have made the series of camera-lucida drawings shown in text-figure 49, from the equatorial region of the seed. These include all the best-known forms, the seeds of *Cycadeoidea dacotensis* and of *C. excelsa* and *Jenneyana* excepted, as mature forms of these have not so far been found well enough conserved to permit such drawings; though it can be seen from their general form and amount of testal development, which are well known, that they too agree within generic limits.

In comparing these drawings it must always be remembered that the seed wall is a more or less appressed one, as the result of inclosure by the five or six to as many as eight or ten interseminal scales forming the pocket in which the seed lies. Also, both outer flesh and stone normally thicken markedly toward the shoulder and about the basal region of the micropylar tube to form a ribbed or even-tentacled *corona*. But while these *coronal ribs* may tend to disappear in some species, or may somewhat conform to surrounding scales, *an original and fixed number is in reality always present and representative of the species.* Furthermore, the ribs may even send up a low crown of tentacle-like projections about the base of the micropylar tube, though it is only after studying the sections very attentively that one comes to see this feature, which, could one see a loose seed, would be very distinctive indeed. In short, we have to do with somewhat appressed vestigial lobes as unmistakable as those of *Physostoma.*

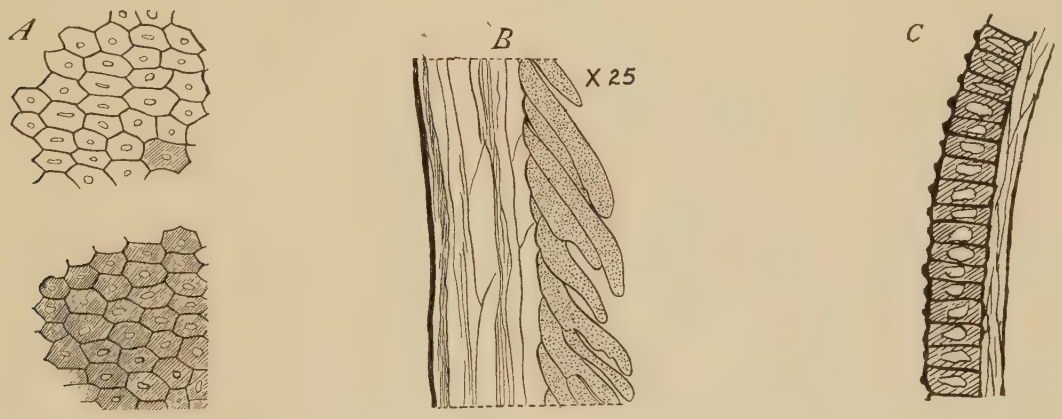


FIG. 50.—Comparison of sclerotestal features in the very similar Cycadeoid and *Lagenostoma* seeds and the quite dissimilar *Physostoma.*

A. *Cycadeoidea Dartoni.* Tangential section through the sclerotesta. × 88. The basal walls of these cells are far thicker than the lateral and tangential walls; the cell interior varies much in appearance, or only the solid base may appear. Again, the outer face may show a marked central concavity.

B. *Physostoma elegans.* Longitudinal view of seed wall exactly showing the "blow off" layer as stippled-in cells to the right, but slightly generalizing the complex fleshy tissues between this layer and the nucellar sac, which appears as a dark line to the left. Original drawing introduced to show the droop of the "blow off" layer as a peculiarity also seen in *Cycadeoidea.* In other respects interesting as a seed of ancient and complex character, between which and *Lagenostoma* there is in actuality a much greater structural gap than between this latter and the *Cycadeoidea* seed type, although the seeds of all three must be regarded as having analogous structures. × 25.

C. *Lagenostoma Lomaxi.* Longitudinal section from above the cupule, showing the inner flesh and mid-sclerenchyma with peg-like projections on tangential wall suggesting that an outer "blow off" layer may have failed of conservation. The structure is essentially similar to that of the most reduced of the *Cycadeoidea* seeds, as shown in Fig. 52; although about in proportion to the size of the seed both flesh and sclerenchyma are much thicker. × about 40. (Redrawn from Scott.)

LATERAL TESTAL COMPONENTS.

The seed stems give rise directly to the testal components, as shown in the transverse section, Figure 48. The elements of the testa here take their origin, the section passing precisely through the transition region where the radio-symmetric seed-stem bundle passes over into the seed-base and testal structures. The xylem (X) is exactly on the point of expanding to form the cup-shaped base of scalariform tracheidal tissue supporting the nucellus, though still deeply inclosed by the fundamental tissue of the seed stem. In the mass of the latter, however, various resin cells characteristic of coniferous seed-base tissue (*Sequoia*, etc.) begin to appear, and peripheral groups of small cells basal to the inner flesh lie next to the conspicuous zone of resin-filled cells (C). The latter gives origin to the middle zone of the testa and is strictly homologous with the gymnospermous "middle stone," though taking precisely the same mineral stain as the resinous cells scattered in the ground tissue about X. The third concentric layer, A, also a single cell in thickness, must be the continuation of the endodermis of the seed-stem bundle; it gives rise to the true outer flesh analogue, in this seed none other than the so-called "blow off" layer of the Carboniferous seed ferns. Finally, the rapidly thinning and fraying zone of large, stringy tubular cells (T) is noted as the well-conserved continuation of the cortical region of the seed stems, which takes origin on the strobilar receptacle as a much thicker zone of small cells.

As already observed, the "*enveloppe tubuleuse*" (Fig. 48 T) of Lignier, or cup-like husk formed by the extension of the cortex of the seed pedicels all round the seed base, tends to disappear. The complex structure of this envelope has been conserved with diagrammatic clearness in *B. Morierei*, where it is seen to consist in an underlayer, the "*assize plissée*," the base of the "blow off," and a distinctly tubular outer layer which is not found continuous all over the surface of the seed, though its cells are markedly susceptible of preservation. But the amount of this tubular-celled tissue varies much in different species. Figure 52 (section 761) is an accurate enough drawing of an American seed in which too few tubular cells to show appear to rest on the middle stone, while there is no appreciable preservation of the inner part or "*assize plissée*" and its apical continuation as a strongly palisaded tissue, the "*assize rayonante*" or "blow off." This condition is, however, exceptional, only one species showing so much reduction.

In examining transverse sections of American species a doubt may arise as to whether the outer layer of the seed is not actually confluent with the interseminal scales, as Solms supposed it might be in places ("Stellenweise") in *Bennettites Gibsonianus*. But this, it is thought, may be due in part to the fact that there are in the interseminal scales groups of subepidermal cells much like the tubular cells of the seed cortex or outer "*enveloppe tubuleuse*," and that, moreover, there is often next the seed an exceedingly thin extension of the epidermal layer of the interseminal scales. There can be no final doubt as to where the seed wall ends and the inclosing scales begin.

MIDDLE STONE.

Following interiorly to the outer flesh analogue or "blow off" layer as so much subject to variation to form ribs and coronal appendages characteristic of the various species, the middle stone is found far more constant; yet the figures 49 C and D, from seeds of one and the same cone of *Bennettites Gibsonianus*, at once show that this layer also shares in rib formation and regionally varies much in the size of its cells. Its thickness as dependent on ribbing varies from one cell in the lateral region to several or more cells as the ribs form in the upper and shoulder region of the seed and converge towards the micropylar base. With regard

to the ribs, it is important to observe that while readily determinable on the seed shoulder, they are much sharper in the micropylar region, where, in addition to the major ribs, there is also a distinct suggestion of minor ribs, well seen in very young seeds. These would, of course, correspond to the midribs of component testal elements which, as best determined from the stone, plainly must unite edge to edge to form the major ribs, just as must unquestionably be the case in all the ancient ribbed seeds.

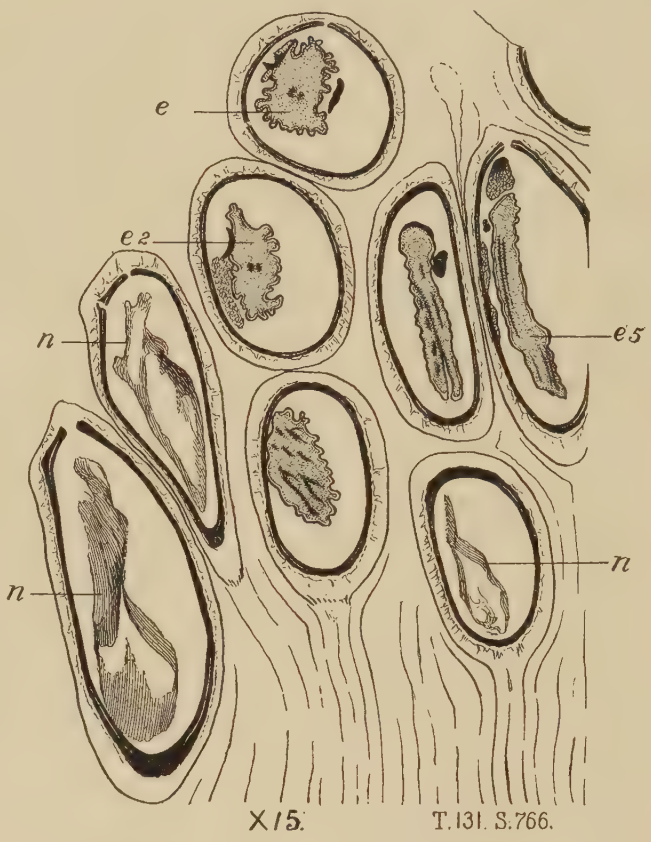
FIG. 51.—*Cycadeoidea Wielandi* (*cf. C. McBridei*). ×15.

Part of a somewhat oblique section through a strobilus of Yale trunk 131, cutting nine seeds at angles varying from nearly transverse (*e*, *e2*) to tangential longitudinal (*e5* and *n*). Illustrates the embryos and embryo-bundle system. The position of the several seeds is quite obvious: *e* with its embryo is cut high up just where the cotyledonary node gives off the two supply bundles for the cotyledons; *e2* passes lower, but is still rather near the cotyledonary plate, since neither radical nor sinus between the lamina appears, while in the seed *below e2* the upper part of the pedicel is cut and the forking of the bundles in the tips of the cotyledons is evident; *e5* and the seed alongside it are cut tangentially, though in each both cotyledons appear.

In each of the seeds *e*–*e5* a lateral deeply stained mass of endosperm (?) appears beside the embryo. In three of the seeds the embryo fails wholly of preservation, but the nucellar sacks (*n*, *n*, *n*) are distinct. Collapse and folding of these sacks is of interest in connection with various forms of nucellar sack rupture in many *Cycadeoidea* seeds.

The characteristic make-up of the seed wall again appears as in the preceding figure, as well as the important additional fact that breaks or gaps in the inner flesh and middle sclerenchyma quite regularly occur near the shoulder and conclusively indicate that these seeds of *Cycadeoidea* are as truly ribbed tentacular or apically lobate as any members of the *Lagenostoma* group.

It is probable that these embryos have undergone some shrinkage, though the cell structure is often clear and does not show much evidence of collapse. However, various remnants about the sides of the embryos indicate unused parenchyma. The appearance does not entirely reconcile itself with the large size of the proembryo, *seen in another species*.



In the American species the stone layer is usually very thin, but quite distinctly indurated, silicification in reality showing density of walls better than other types of conservation. The cells of the stone superficies appear to have had a very thin tangential wall, even subject to collapse, so as to sometimes simulate a series of flattened hexagonal cups with very heavy bottoms and sides thinning a little toward the top. In the French specimen it is the cell contents rather than the cell walls that appear to have "taken the stain," and this produces a certain appearance as of a decidedly fleshy tissue, especially in the outer cells bearing the "*blow off*." But what the true nature of the tissue is can not rest in any doubt; for it is, as we see, often highly indurated in the American specimens, and nearly as much so in the Isle of Wight specimen; while, as I fully believe, the slightly less indurated condition seen in the inner part of the midstone of *Bennettites Morierei* is quite exactly paralleled by the middle layer in *Pinus resinosa*. In considering any mineralized tissues, moreover, it is occasionally necessary to note that the staining could exhibit the cell contents rather than the cell walls, which might finally fail of clear outline and be replaced by structureless mineral.

INNER FLESH.

The inner fleshy layer or tissue region lying between the stony region and the nucellar sack is of about the same breadth as the stony region in all the Cycadeoideæ, bearing in mind the reduced testa in the American *C. Wielandi*, where both these coats are very thin. In no instance, however, is the inner flesh distinctly enough conserved in the lateral region of the seed to permit camera-lucida drawings, or even photomicrographs showing it other than as a clearly outlined zone of soft, crushed tissue. But in the Normandy seeds preservation is often diagrammatically clear near the seed base where this zone is from three to about

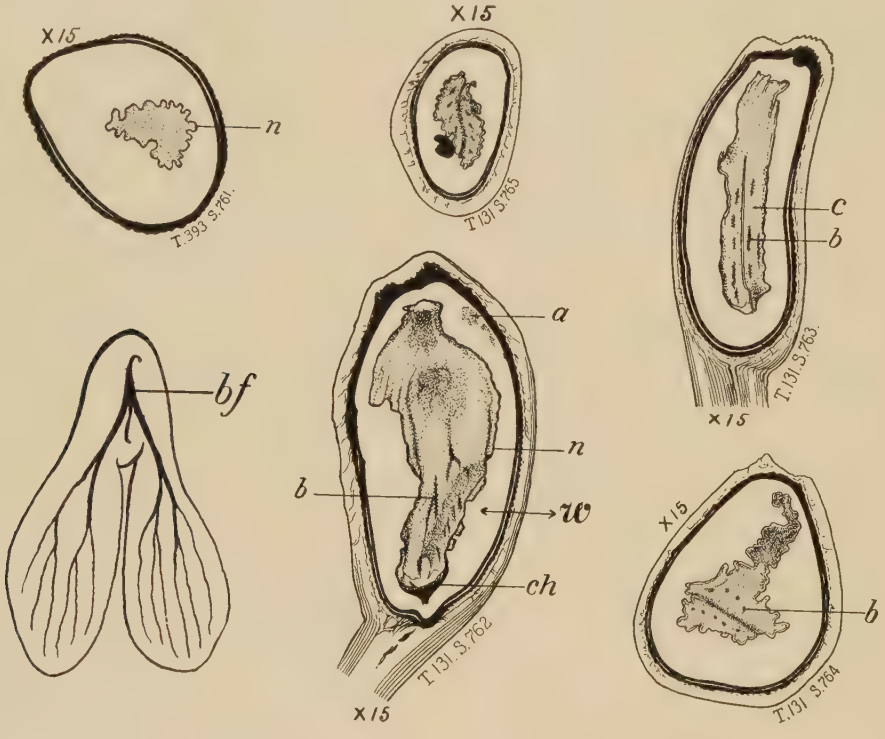


FIG. 52.—*Cycadeoidea* seed structure—continued. ×15 or less.

Four subtransverse to sublongitudinal sections of seeds from Yale trunk 131 (*C. Macbridei ?*), together with an obliquely transverse section of a seed from trunk 393 (*C. Wielandi*) and the diagrammatic view of embryo (*bf*). These figures are all drawings made just as the artist saw the seeds. The inner flesh is shown as a smooth line, the middle stone as a finely notched black line, and the outer flesh or more exactly the "blow off" layer as a light zone. Exterior to this lighter "blow off" is the so-called "tubular layer" which rises from the seed stem as a sort of basal cup or husk. The ribbed character of the seed wall again appears, although less obvious in the seed from trunk 393 (S. 761) which has an unusually thin wall with very little trace of an outer flesh. The nucellus (*n*) is usually seen to cling to the somewhat shrunken embryo. The embryo characters are, however, very satisfactorily seen, the bundles (*b*) of the young cotyledons (*c*) being plainly indicated. At *a*, section 762, traces of tissue apparently extra-nucellar, and not albumen.

seven cells deep, with the outer cells elongate, and flat squarish to rounded forms on the interior. The nature and succession of the testal elements is clearly illustrated in the transverse section through the radio-symmetric seed base shown in text-figure 48, where the relation to the central bundle is still clear and the layers appear in their initial and simplest form. That the ancestral endosarcal bundle system is not entirely eliminated is probable, though final determination of this point still depends on favorably located rib-angle sections of exceptionally conserved seeds.

SEED TIPS AND MICROPYLAR TUBE.

The tips of the seeds must be searched for. Though in general the outer form is well conserved, histologic details are usually less distinct. Owing to the small size of the micropylar tube and, if one pleases to so call it, the terminal stigmatic funnel, complete median longitudinal sections are rarely secured, the more so because the seeds vary considerably in size from base to summit, and within certain limits in their compression surfaces, however certainly they conform to the general major and minor rib development for the given cone or species. In consequence there is required for a clear picture of the seeds a considerable number of photomicrographs sufficiently enlarged to bring the micropylar tube features into full view and yet permitting the reproduction in plate form of fairly extended areas of the sections without taking up undue space. For this purpose 10 diameters seems most convenient. As reference to the Plates 51 and 52 shows, the stigmatic surfaces and tubes are not the rare objects they appear to be at the higher magnifications. Every few millimeters some view of a micropylar tube may be had; and it is of particular interest that in nearly all the longitudinal sections of bract-inclosed cones, owing to the variation from the true vertical median plane, many transverse sections of the micropylar tubes are present and even the terminal funnels are in some instance seen to be surrounded by interseminal scale heads just as in a true surface view on tangent section. Crowding or slight curving of the micropylar tubes by the interseminal scale heads is also a lesser cause of variation from the normal. It is thus readily understood that, however careful the sector, he ordinarily secures only approximately median longitudinal sections of either cones or seeds. But there is, as just related, the interesting compensating fact that because of strobilar furrowing due to the appression of inclosing bracts, small parts of the lateral surface of the cones may even appear in the longitudinal sections of cones; and such sections are in reality much richer in details of micropylar tubes than might at first be expected. In fact, so far as concerns tube structure, they scarcely require to be supplemented by transverse sections. Owing to the peculiar structure of the Cycadeoidean ovulate strobilus and precisely because of slight variations from the normal, the sections of any considerable size nearly always afford full details of the macroscopic features of the entire sporophyll. The longitudinal sections often afford transverse views of seed stems and, as just seen, are rich in nearly complete details of the seed apex and micropylar tube, while the transverse strobilar section yields in passing from center to periphery virtually the same result as could be had by serially sectioning a single sporophyll from its insertion to the apex of the erect terminal seed.

To select well-conserved cones and cut sections varied from the transverse and longitudinal directions to the very best advantage is another matter. Such, of course, somewhat spoil the cone for the larger complete sections, and also require to be very thin in order to show the highly sclerotized tissues of the peripheral region of the strobilus to advantage. But few such sections have been made. It is desirable to make more and the series is still being added to in order to secure drawings of the entire seeds showing the complete histologic features. In the present descriptions no attempt is made to say the last word.

Certain it is that a few American silicified cones show the entire structure as perfectly as the ferrized cone *Bennettites Morierei*. A few such are borne by the Yale specimen 393 and several others, and further examples are to be found amongst the numerous *C. Dartoni* cones; but so far by some peculiar disfavor of chance a true median seed section has not been obtained from any of the cones of more perfect conservation. In several instances where new material was carefully selected and oriented the sector failed, so that the effort to get further sections from the rare perfect cones remains to be renewed.

Meantime, on the basis of the less perfectly conserved sections already at hand, the characters of which are clearly illustrated in the plates, a nearly complete picture of the several specific forms of micropylar tube may be had. And in fact the micropylar structure holds a special interest since the observation by Miss Berridge (1911) and Mrs. Thoday (1911) of certain curious resemblances to *Gnetum*. (See Fig. 54.)

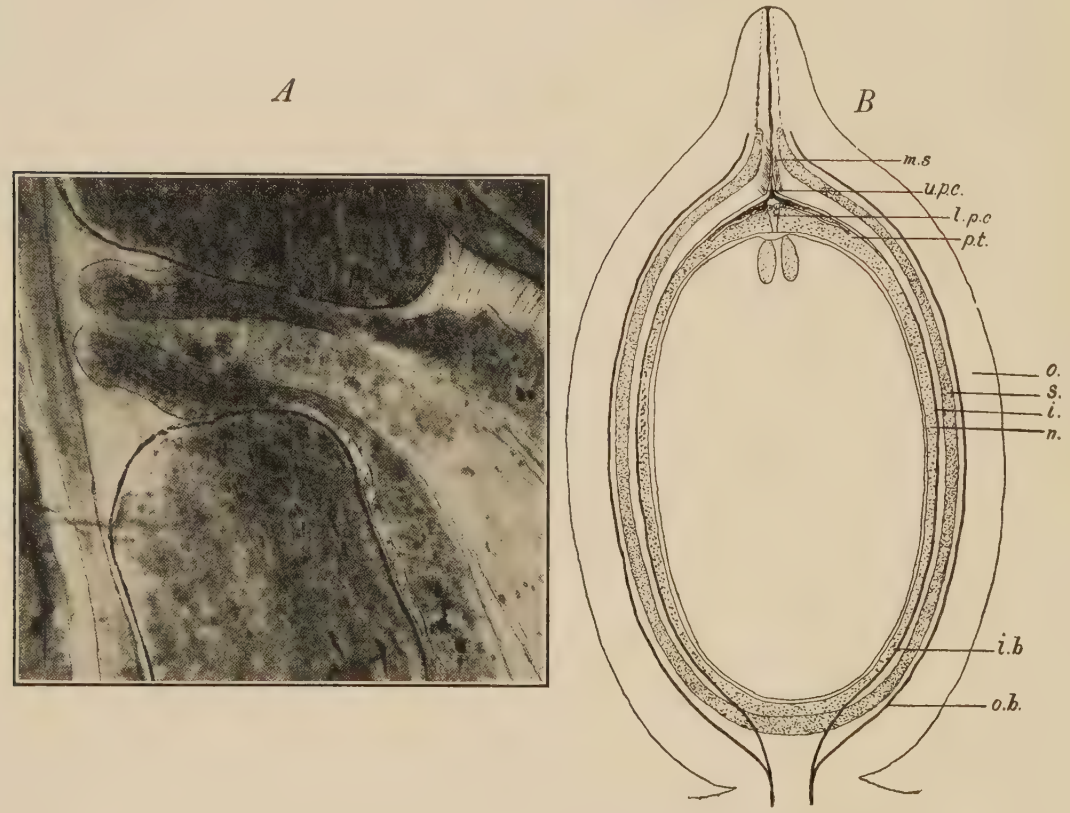


FIG. 53.—Micropylar region of *Cycadeoidea* and *Bowenia* compared.

A. *Cycadeoidea Dartoni*. Shoulder and micropylar region of seed (containing embryo) in median longitudinal section with adjacent interseminal scales and enveloping bract. × 100.

B. *Bowenia spectabilis*. Longitudinal section of ovule (diagrammatic, from Kershaw): *o*, outer fleshy layer of integument traversed by outer bundle series, *o.b*; *s*, stone layer; *i*, inner fleshy layer traversed by inner bundle series, *i.b*; *n*, nucellus; *p.t*, pollen tube traversing inner flesh; *l.p.c*, lower pollen chamber; *u.p.c*, upper pollen chamber; *m.s*, sclerenchyma round micropyle.

In the first place, it should be noted that the slightly retouched photomicrographs of a seed of *C. Marshiana* (*C. dacotensis*) shown in Volume I, Plate XXVIII, Figure 2, is an excellent figure in every respect, and plainly shows a short-stemmed, erectly borne seed with a very short non-curved micropylar tube, formed by the extension of the lateral testal walls all the way to the seed tip, which shows no marked terminal flange. Although the nucellus extends far into the base of the tube, it does not pass on beyond the testal walls; and in general this must be the condition in the several other species. These relations, however closely in agreement, are less obvious in *Bennettites Morierei* and *Gibsonianus*, *Cycadeoidea Dartoni*, *C. Wielandi*, etc. In these the testa thins out suddenly at the base of the usually long and curved micropylar tube, and the ribbed character is less obvious, the tube contours appearing quite symmetrical nearly to the tip, which is again rayed and even pronouncedly flanged, so that in seed after seed there may be doubt as to the testal rib continuity. Nevertheless, as the ribs of the canopy region persist far up, a series of sections showing the exact

structure of the seed tip would doubtless indicate that even after the testal ribs end superficially there are always still left structural features, more or less analogous to ribs traversing the more or less rayed and flanged micropylar wall, all the way to the tip. So one must be prepared for those slight differences of appearance noted in what are essentially equal views. (Compare Figures 46, 47, and 53.)

After patiently studying various true median sections of the micropylar tube, with the structures more or less imperfectly conserved, it is found that the flesh and stone of the testa normally continue as the tubular wall of about two cells in thickness, with an outer terminal covering or flange of palisaded tissue possibly arising from the "blow off" layer of the seed, or at least from the final testal extension. The resemblance in outer form of the more or less pentagonally flanged micropylar tube-opening to that of *Gnetum gnemon* and *G. africanum* is all but complete, since in the latter the inner integument, once free of the nucellus, passes clear as the micropylar tube and then forms a terminal flange overcapping the extreme summit of all that more basal part of the tube wall arising from the testa proper.

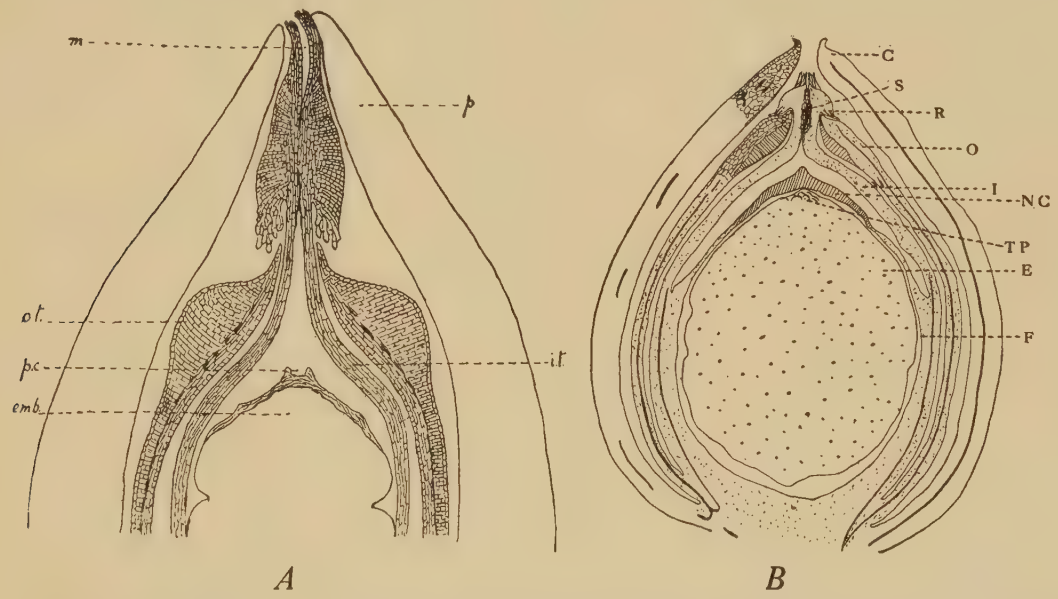


FIG. 54.—Longitudinal sections of gymnospermous seeds—continued. The *Gnetum gnemon* seed with that of *G. africanum* as connecting links between the much-reduced Cycadeoid seeds and those of modern cycads.

A. *Gnetum gnemon*, longitudinal section through upper half of young seed. *p*, inclosing cupule or perianth homologous to the *Lagenostoma* cupule; *ot*, homologue of the palisaded or "blow off" layer of Cycadeoid and older seeds, together with sclerotesta; *it*, inner integument; *pc*, pollen chamber; *emb*, embryo; *m*, micropylar tube. ×25. From Berridge.

B. *Gnetum africanum*, longitudinal section through seed. C, outer cupular covering; O, outer integument or sarcotesta; I, inner fleshy integument; F, fused nucellus and inner integument; E, corrugated endosperm; TP, tent-pole; NC, nucellar cap; S, closed micropyle; R, drooped micropylar flange. Enlarged. From Thoday.

The mature tube is filled nearly to its end with what may be cancellated or lysigenous, that is, broken-down, nucellar tissue, as in *Gnetum*. The extreme end of the *Cycadeoidea* inner integument never quite extends beyond the outer integument or comes to form a final capping of the micropylar tube as in *Gnetum gnemon*. But it might be in nowise incorrect to say that the interior layer of the micropylar tube is formed by the extension or beak of the nucellus as it rises above the pollen chamber. While, therefore, it is interesting to find that both the testal wall and the nucellus join in growing forward to form a well-marked tube, the final part played by each in walling this tube *seems merely one of degree*, testal growth or nucellar extension apparently being equally competent to play the needed rôle.

It thus appears that the condition in the *Cycadeoidea* seed would make it easy to develop a capped micropylar tube like that of the cupule-inclosed *Gnetum;* there is here a structural likeness inviting some form of explanation. Perhaps the similarities in question may be the simplest of adaptations rather than long-retained characters restricted to the present forms and indicating their close relationship. In either case megaspore protection is the object to be accomplished, and there is no apparent reason why this similarity of type might not arise independently. The Cycadeoidean form seems the older.

In reality, what at first sight does seem more suggestive of relationship is the striking likeness in the development of the "blow off" in *Gnetum* and *Cycadoidea*. But here again general similarity of testal development and reinforcement in the shoulder region may be mainly due to inclosure of the seed—in the one case by a cupule, in the other by radially disposed interseminal scales; for it should be borne in mind that both the seeds before us are relatively modern forms which have long since lost the complex apical chambering surely once present, and which in the course of post-Paleozoic reduction and change might well accentuate certain acquired features. Other forms presenting intermediate conditions to those already observed are certain to be found before many years have passed. Then, too, are the *Gnetum gnemon* and *africanum* seeds taken by themselves more like those of the Cycadeoideæ than is the seed of *Biota orientalis* with its *Trigonocarpus*-like form and very distinct although hairy shoulder development of the "blow off"?

Doubtless the larger floral features and especially the arrangement of parts in *Gnetum* do suggest a certain marked kinship to the Cycadeoideans, although in seeking out the points of ultimate resemblance it is well to guard against laying all stress on features that may recur in other gymnospermous forms. To the larger aspects of this subject, however, it will be more convenient to return later on in this chapter. The features just noted are so interesting and instructive from a botanical viewpoint that they easily merit the present briefer discussion in immediate connection with their description.

HOMOLOGIES OF THE CYCADEOID SEED COAT.

In Volume I (p. 174) the view was taken that *Lagenostoma* presents the nearest known analogy to the seed-wall structure of *Cycadeoidea* of any form existing or extinct, and no reason is now seen to recede from this view; for in reality *Lagenostoma* offers (in the retention of reduced inner flesh bundles, or an endovascular condition) an intermediate stage between the large, thick-walled amphivascular seeds of existing cycads and the reduced or even truly monovascular *Cycadeoidea* seeds, while the archaic features in the apical region of the latter must be of far more significance than would be the retention of the testal bundle system, which was without a shadow of doubt anciently present; and the closer *Cycadeoidea* is studied the clearer does it become that, despite an inclosed position and despite reduction, the seed apex is after all of the ancient multilobate type. Further, it may be accepted that the stony palisaded layer of *Lagenostoma Lomaxi*, though following ripening and shedding of the seed, the external one in all the lateral region is none other than a middle stone. The small tubercles of this layer (*cf.* Fig. 50 c) were thought by Oliver and Scott (1904) to have supported an outer covering of thin-walled cells, while in the *Cycadeoidea* seeds one may plainly see that the thin outer wall of the outer cells of the stone layer functions as a bearing wall for the "blow off" envelope. In comparisons with *Lagenostoma* it must be emphasized that various species are known, and that in *L. ovoides* for instance, where both cell form and preservation suggest decided resemblance to *Cycadeoidea*, the indurated layer is several cells thick. There is, therefore, in both these genera marked similarity in the considerable degree of variation in thickness and development of the stone layer, although to some the

Lagenostoma cupule may seem to prevent comparison. It should, however, be recalled that this latter structure must have been subject to either reduction or non-development, whereas the tubular layer which occupies the same region in *Cycadeoidea*, and serves the same essential function as a basal cup or husk, must also be a last remnant of some ancestral leafy structure. Moreover, it is unlikely that there is any more difference between a seed with or one without a cupule than there is between a naked flower and one with a campanulate corolla. Just as calyx and corolla are the sterile leafy envelope of the angiospermous flower, so must the cupule be the sterile leafy coat of the ancient seed.

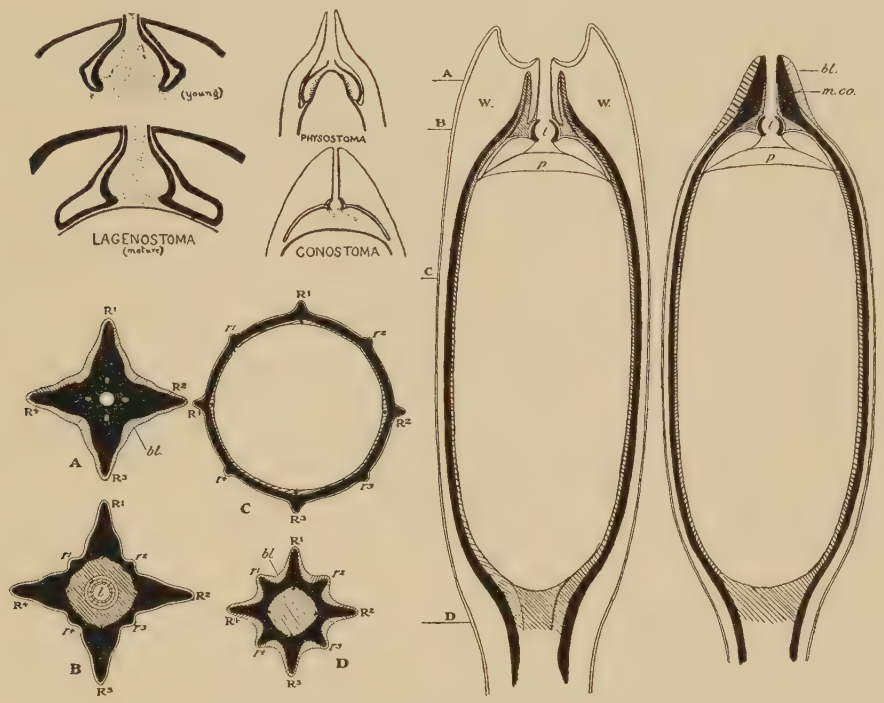


FIG. 55.—Gymnosperm seed structure—continued.

To the right, restorations of the tetramerous "coal ball" seed *Conostoma anglo-germanicum*, in longitudinal section through opposed pairs of major and minor ribs. The ribs are shown as they appear at the heights A, B, C, D, in the attached transverse sections correspondingly lettered, R1–R4 being the major and *r1–r4* the minor ribs. In both longitudinal and transverse sections the vascular bundle and nucellar wall are represented by a single line. The hard testa and lagenostome are solid black. The "blow-off" covered, rib-formed wings (W) are in white. Parenchymatous tissue shaded. *bl*, "blow off;" *m.co*, micropylar cone; *l*, lagenostome; *p*, plinth *projected*. × 12. The true relation of the lagenostome to the canopy is shown to better advantage in the four supplementary figures showing the condition in *Lagenostoma*, both young and mature, *Physostoma*, with a medium-sized lagenostome, and *Conostoma*. (Compare with Fig. 46.) From Oliver and Salisbury.

So far as now recalled, *Polypterospermum* of the French Paleozoic is the only other ancient seed which has ever been suggested as offering a distinct likeness to the Cycadeoidean seed structure. Professor Lignier (1894), in studying the four (occasionally five) ribbed *Bennettites Morierei*, after pointing out marked testal resemblance to *Gnetopsis*, attached too much significance to apical appendages, somewhat wrongly reaching the conclusion that the latter seed presented no true analogy; but he went on guardedly to name an apparently related form, *Polypterospermum*, as probably much nearer to *Cycadeoidea* than other ancient types, a suggestion of relationship which seems to have been little heeded.

However, further interesting comparisons with ancient seeds have been much aided by the instructive interpretations of *Paleozoic* seed structures and noteworthy study by Oliver and Salisbury (1911) of the two species *Conostoma oblongum* and *C. anglo-germanicum*.

In the species of *Conostoma* no cupule obscures the exosarcal features, but the seeds have the small size of those of *Cycadeoidea*, in consequence of which they present much difficulty of study, due to dependence on chance sectional planes. Nevertheless, by plotting about a score of sections of *Conostoma anglo-germanicum* and nine sections of *Conostoma oblongum*, and then constructing models from the estimated planes of the sections, nearly concise restorations of both species have been obtained. Both are endovascular, the inner fibrous flesh being traversed by six bundles in the angles of as many simple ribs in *C. oblongum*, and four bundles in the angles of the four major or wing ribs which initially alternate with as many minor ribs in the somewhat more complex *C. anglo-germanicum*. Both species thus agree with *Cycadeoidea* in size and in being coronate radisopermic ribbed and winged forms with essentially the same wall structure, barring retention of the endosarcal bundles, traces of which are, however, yet likely to be found in the Cycadeoideæ.

Indeed, truly essential testal and apical differences, rather than likenesses, remain to be established, now that we know *Cycadeoidea* to be a characteristically four- and five-ribbed and lobate, winged, tentacled seed which also shows some tendency to alternation of major and minor ribs.

Evidently *Cycadeoidea*, though of composite type, has, as befits its Mesozoic extinction, a clear title to admission into the great groups of Paleozoic gymnospermous seed types retaining indisputable evidence of a yet more ancient multiple integument. And this is yet more strongly indicated when we turn to the fuller lobed *Neuropteris heterophylla* seeds described as attached to their foliage by Kidston, if, indeed, these are true megaspores. Especially so, if we further consider that most remarkable six-lobed microspore-bearing fruit *Codonotheca*, of quite the same size and outer aspect as the reputed *Neuropteris* seeds, and on the score of association strongly suspected to be of Neuropterid affinity when first described (1903).

Re-examination of this fossil by the writer has so far failed to establish the presence of sporangial structures on the inner surfaces of the campanular lobes, where much loose and extraordinarily large-sized pollen may be seen, seemingly in quite the position in which it grew. As these Codonothecan or Neuropterid microspores or *prothallate pollen* grains are the largest known, even greatly exceeding *Stephanospermum*, it, however, remains quite possible that by some modification of Nathorst's chemical method some evidence of extensive prothallial tissue may be found. While the general appearance at first seemed to preclude the drifting in from the outside of pollen attaching itself to sticky inner surfaces of free apical lobes of a small central seed and there undergoing prothallial growth, such an interpretation is, because of the peculiar spindle-shaped and possibly ovulate base, not easily dismissed. Should this prove to be the true interpretation of *Codonotheca*, it is the most leafy of known seeds; but any one is free to work out various alternative interpretations for himself, and certainly this singular fruit would be at once explained by many, or most, as some entirely primitive form of giant microspore case had not the ubiquitous staminate disks of Mesozoic times led us to expect to find circular emplacements of sporophylls in process of reduction in ancient plants, and in particular taught us to see that in such disks spores once borne ventrally may easily become falsely dorsal. In any case, however, the study of such forms must ultimately shed much light on the nature of gymnospermous testal structure, the essential and primitive elements of which already begin to appear.

But yet another comparison of the seeds of *Cycadeoidea* may be made with forms far nearer at hand that might have been thought of before. Through the great kindness of Professor R. B. Thomson, whose excellent demonstration of the megaspore membrane of

the gymnosperms (1905) is well known, I have come into possession of a beautiful though limited series of longitudinal sections of existing gymnospermous seeds; and the attentive study of these shows that the smaller seeds, especially of the Abietineæ, present a clear analogy to *Cycadeoidea* in all that pertains to lateral wall structure. In *Pinus resinosa* there is, taking the lateral wall, a noteworthy parallel, and if one had before him a complete series of both transverse and longitudinal sections of the abietineous species, it is likely that traces of apical ribbing would be found and that a composite exceedingly like *Cycadeoidea* could be observed. The Cupressineæ (*Biota orientalis*) also afford points of resemblance.

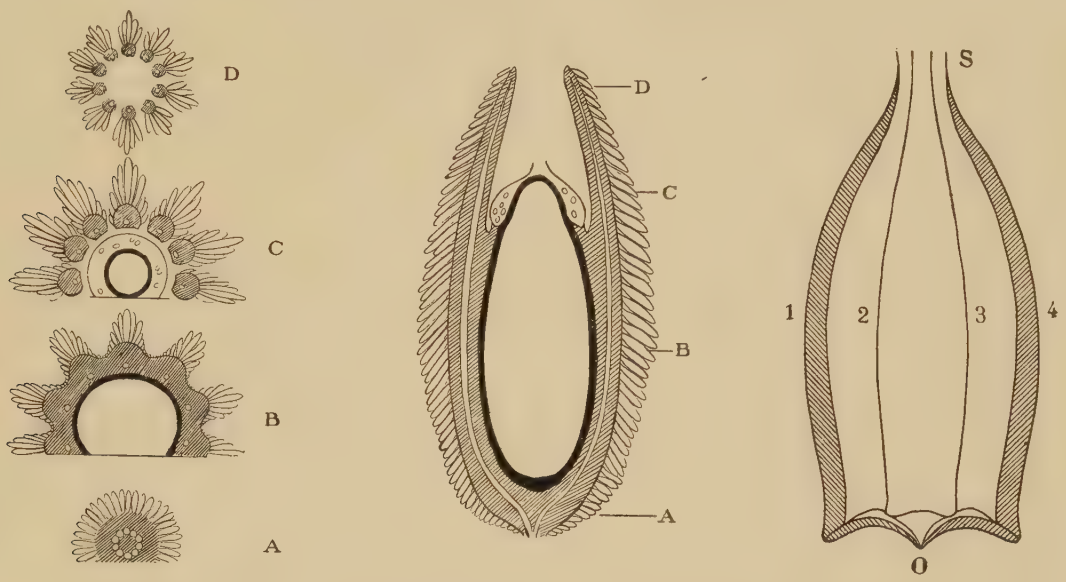


FIG. 56.—Diagrammatic drawings of diverse types of ancient seeds.

A–D. *Physostoma elegans* of the English "coal balls" in median longitudinal and transverse sections as respectively lettered. Integument enveloped by drooping cells of the "blow off" obliquely shaded, with vascular strands unshaded and the secretory zone next the tapetum in solid black. Inside the lagenostome various pollen grains. A decamerous seed. ×15. (From Oliver.)

OS, a bilateral hexamerous seed attributed to *Neuropteris gigantea:* 1, 4 the major, and 2, 3 the minor ribs. O is the insertion-point and S the summit. About twice the natural size. *Terrain houiller du Nord*, France. Seeds associated with this form, which is very similar to the coal-ball seed *Hexapterospermum Noeggerathi* (Williamson 1875, Fig. 115, *a* and *b*), distinctly recall the *Codonotheca* campanula and may, like it, be microsporous. (From Bertrand.)

This line of study promises much interest, for the Abietinean series was always regarded as a quite modern side branch rather than an old gymnosperm stem terminal until the possession of really ancient structures was pointed out by Hollick and Jeffrey (116). These writers, in their admirable study of Cretaceous conifers, show *Pinus* to be archaic, and demonstrate a new genus *Prepinus* of more primitive structure than any other conifer living or extinct, while Jeffrey insists without reservation that the Abietineæ are the oldest tribe of conifers. The decided resemblances in the seed-wall structure to *Cycadeoidea* lend further color to such views, if any value can be assigned to present-day features of gymnosperm seeds in trying out questions of ancient relationships amongst great groups of gymnosperms, using the name in any wide sense.

Generally speaking, comparison of the seeds of *Cycadeoidea*, as so evidently derivable from ancient monovascular and ribbed types, is more readily made with coniferous and Gnetalean seeds than with those of existent cycads; though it is not meant to suggest even remotely that this fact alone implies any markedly close relationship of Cycadeoids to conifers. Probably undue significance may very easily be given to the presence or absence of an outer bundle series, to the presence or absence of cupules, and doubtless also to the

degree of fusion between the nucellus and inner flesh. Dr. Kershaw, who has made a study of the structure and development of the ovule of *Bowenia spectabilis* (1912), reasonably finds a general structural agreement with seeds of the *Medulloseæ*, *Trigonocarpus*, *Stephanospermum*, *Cardiocarpus*. It is found that the vascular supply of the *Bowenia* is afforded by one foliar bundle of the sporophyll which divides into an outer ring of 7 to 9 unbranched collateral mesarch bundles and an inner series of branched concentric bundles. A seeming anomaly of the inner series is an occasional branching into the free portion of the nucellus. The seed is then, with the exception of this latter peculiarity, typically amphivascular. It is found, however, that despite the fact that the cycad integument has every appearance of a morphologically double structure derived from fusion of a single integument with a cupule along the line of the middle stone (Stopes, 1905), the integument of *Bowenia* develops homogeneously and only gradually segregates the three characteristic layers—the inner flesh, middle stone, and outer flesh. So far as known, the other cycad genera agree in this uniform testal development, which might be held to preclude any close relationship with a monovascular cupule-inclosed seed like *Lagenostoma*, more especially because of the tendency of the small bundle branches of the inner series to run up into the free basal nucellar tissues, as just mentioned. The further fact is also adduced that while the bundles of the inner series in cycads are of subconcentric structure, with little phloem and ramose, the integumentary bundles of *Lagenostoma* in equivalent position are collateral-mesarch and unbranched, unless at the very tip of the integument a forking occurs.

The more nearly the evidence for an adequate theory of seed origins which has accumulated in the last few years is brought together, the more certain does it become that anatomical variations like those just cited can not in themselves indicate remoteness of either origin or relationship. They are differences which are hardly sufficient to separate families. No one has been inclined to attach much significance to the free or fused character of the nucellus, as probably due to the mode of ovule growth (1903); and so far as theoretical cupule fusion is concerned there is no lack of analogy either among gymnosperms or angiosperms.

Similarly, while a few spiral tracheids may have much significance as vestigial traces of a former bundle system in certain situations, such importance can scarcely pertain to the small bundle branches observed at the base of the *Bowenia* nucellus. The fact that the inner flesh bundles characteristically branch indicates that the very first branch given off into the basally fused tissues of the nucellus may be secondary. At least it is not probable that the small traces are ancient and lost in older seeds, though still retained in *Bowenia*. Furthermore, all the *Lagenostoma* structures, though of ancient stamp, are, as compared with existent cycads, greatly reduced or of slight development, while the character of the elements which unite to form the testa is much more visible. In short, it appears that the gymnosperm seed types must stand in some close complementary relationship.

At first sight there seems to be a wide gap between the platyspermic and radiospermic seeds; but from several points of view there is no greater hiatus between the two-angled or platyspermic and the trigonal forms than between the latter and the more highly angled forms. In the first place, the transition between these types is observable in existing Cycads. Secondly, Oliver and Salisbury (1911) observe some flattening in the hexangular *Conostoma oblongum*, and there is much more in the tetravascular *Gnetopsis elliptica*, markedly elliptical in transverse section, as its specific name implies, and presenting close approximations to *Lagenostoma*, perforce to *Cycadeoidea*. Thirdly, it should be pointed out that, if the seed coat is to be looked upon as formed from fused sterile organs, there is relatively no more difference between platyspermic forms than between equitant and ternately inserted leaves.

The ternately constructed seeds are, of course, the key to the problem of relationship between the simpler or platyspermic types and the multiple-angled radiospermic or more complex types; whence it follows that the conception of the seed of *Trigonocarpus* as a derivative of a double whorl of three leafy lobes each must be reckoned with. This form, then, being so elemental to any consideration of the general theory of testal structure, space may well be afforded for Dr. Scott's compact description of *Trigonocarpus Parkinsoni*, in all probability the seed of *Alethopteris:*

"*Trigonocarpus Parkinsoni* is found in three distinct states of preservation in the English Coal-measures: (1) in the common condition of nut-like, somewhat triangular casts, which, as shown by Hooker and Binney and by Williamson, are really internal casts of the seed cavity; (2) as external casts, showing the testa and the true form of the seed; (3) as petrifactions, in which the structure is more or less perfectly preserved. From these various data a fairly complete knowledge of the organization of the seed has been gained.

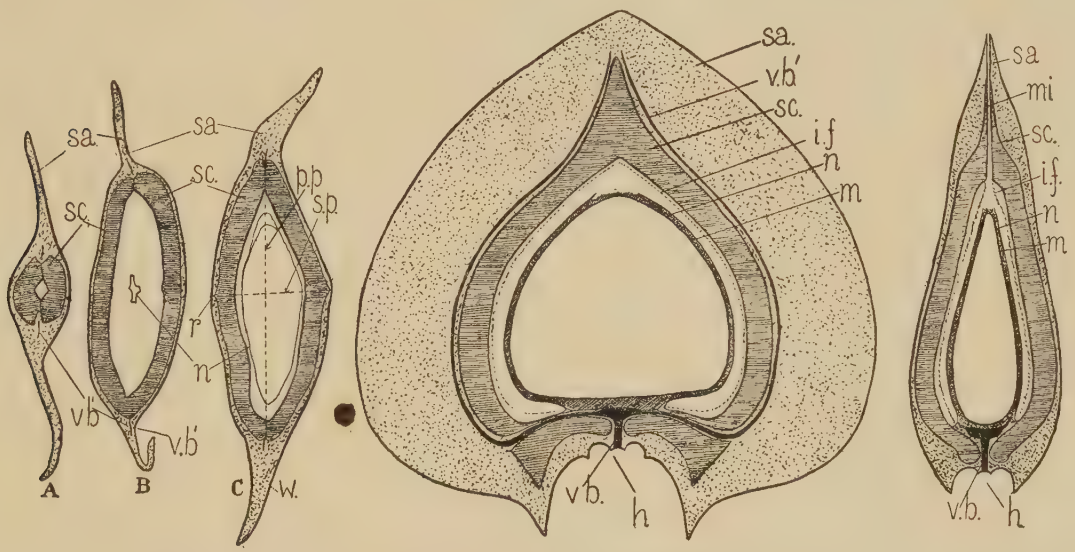


FIG. 57.—The dimerous seed *Mitrospermum compressum* in the major plane longitudinal section, the minor plane longitudinal section, and the basal, shoulder, and apical transverse sections (A, B, C). ×6 or 7. From A. Arber.

In the major plane section the testal relations appear essentially the same as in *Bowenia* (Fig. 53), less inner bundles. The sarcotesta (*sa*) is traversed by the outer bundle (*vb'*), while the sclerotesta (*sc*) is heavy and the inner flesh (*if*) reduced, inner bundles being eliminated. Nucellus and megaspore *n* and *m*. Below the hilum (*h*) project the basal spurs.

In the transverse sections the major plane is extended by the sarcotestal wing (*w*), and the minor plane (*sp*) coincides with the median sclerotestal ridge (*r*). (Compare Fig. 56, *O*.)

"The seed is a very large one, the length reaching 5 cm., of which quite half is accounted for by the enormously long micropyle; the body of the seed has a maximum diameter of over 2 cm. The testa consists of two clearly distinct layers—the outer layer or sarcotesta, composed of delicate, partly lacunar tissue, bounded externally by a sharply differentiated hypoderma and epidermis and the inner-ribbed sclerotesta, constructed, like the stone of a peach, of dense thick-walled tissue (*cf.* Plate 54, photograph 2). The ribs show a very definite arrangement. There are three principal ridges, corresponding to sutures, in the sclerotesta, and usually 3 secondary ridges in each space between the former, making 12 ribs in all; within the sclerostesta there are some traces of an inner soft layer. The nucellus has a definite epidermis, and appears to have been free from the integument, from the chalaza upwards; it terminates at the apex in a dome-shaped pollen-chamber, provided with a long, narrow beak, as in the seeds of Cordaiteæ. The membrane of the megaspore or embryo-sac is evident, but the prothallus has not yet been found preserved.

"The vascular system of the seed is double. At the base six bundles branch off from the common supply strand and pass upwards through the sarcotesta, taking a definite position [so that without further branching a single strand faces each of the two outer ridges of each of the three

triads of secondary ridges]. These bundles appear to have been collateral, with external phloem, and there is evidence that the xylem was mesarch. The inner vascular zone formed a complex tracheal network in the nucellus; near the chalaza the sheath of nucellar tracheides is continuous; farther up they range themselves in longitudinal strands connected by abundant transverse anastomoses. The most remarkable feature of the seed is the long micropylar tube, formed by an extension of the ribbed sclerotesta, and inclosed in a broad, wing-like prolongation of the sarcotesta. It is not quite certain, however, to what extent the flattened form of this part of the seed is natural.

"The seed, with its fleshy and stony coats, double vascular system, and pollen-chamber, is evidently very nearly akin to the seed of a recent Cycad, the chief difference consisting in the free nucellus, whereas in the modern family it is adherent to the integument." [See Plate 54, photograph 2.]

No hypothesis of testal evolution may be called adequate which ignores the possibility of a derivation of gymnospermous seeds without testal bundles, by reduction from forms with bundle-supplied, multiple-layered integuments; and such reductions could just as readily occur in platyspermic as in highly-angled radiospermic seeds. In fact, the varying conditions of bundle and ridge development in the Trigonocarpons alone sufficiently demonstrate the mode according to which sarcotestal bundle reduction must have proceeded, as clearly appears from the following résumé, in part that of Salisbury (1914), showing the extent of reduction in the *Trigonocarpon* group:

(1) *T. Parkinsoni* has a strongly trilobate and fissured sclerotesta enveloped by a non-fissured sarcotesta, curiously alate above, but tri-ribbed below. There are three sets of the minor ribs opposed to three major sarcotestal bundles which bifurcate.

(2) *T. corrugatus* and *T. Shorensis* have the tri-fissured sclerotesta enveloped by a non-comissured sarcotesta, with but one secondary rib in the position of the groups of three observed in the preceding seed. The sarcotestal bundles remain the same, there being two to each minor rib.

(3) *T. pusillus* has the tri-fissured sclerotesta, with the enveloping sarcotesta nearly circular and ribless.

(4) *Pachytesta* has the tri-fissured sclerotesta enveloped by a ribless sarcotesta; but there are two concentric bundle series which exhibit considerable secondary (?) branching and along with a somewhat complex internal structure suggest unequal rates of reduction.

In *Stephanospermum* the sclerotestal ribs are wholly obsolete; but this type might be derived from some hexangular form like *Polylophospermum*. This latter, with *Ptychotesta*, *Hexapterospermum*, and *Polypterospermum*, are the representative hexagonal members of the Trigonocarpeæ.

Sclerotestal commissures evidently result from appressed edges of component lobes, ribbed and bundle-traversed. But conceiving all those seed forms with an inner and outer bundle cycle as essentially double-whorled, it may not be clear whether the component members of the more perfectly fused outer whorl alternate with those of the inner whorl or not. Both conditions are to be expected, if floral envelopes in general offer any analogy. At least, the members of the outer whorl are readily conceived of as arising from the fusion of sterilized or leafy organs, although the apical ridging and also notching of the outer envelope may be quite deceptive as indices for the position of the primitive lobes or leaves. Thus in the *Codonotheca* (*cf.* Figs. 61, 62), to which there is constant occasion to refer, the notches of the hexalobate campanula may really correspond to leaf axes, since the initial six bundles fork uniformly in the mid-region of the chalice and so condition the notches. It is easy to conceive sterilization of such a chalice and fusion with the envelope of some primitive and centrally inserted megaspore. The long course of seed evolution includes whole cycles of change; and probably there can be no greater error in seed theory than the continual requisition of directly evolved new structures. Even if the sarcotesta and sclerotesta consti-

tuted a fairly homogeneous single cup-like structure in the Trigonocarpeæ, the theory of original derivation of *some* seed testas by fusion of double whorls is scarcely shut out; nor is it necessary to conceive these whorls as originating simultaneously. Previous to the known phase in the history of most old seed types there must have been several re-alignments of the leafy parts protecting the megaspore. But it seems that as plants increased in complexity the primitive types of megaspores were produced more and more freely on more and more complex leafy bodies, and that with each major stage of branching new emplacements could result with new phases of sterilization or reduction of leafy organs surrounding and protecting the retained megaspore. Indeed, it is just here and along these lines of inquiry that the study of testal homologies and origins logically leads to that of cone and flower structure, as will be more definitely shown in the concluding section of this chapter.

DUAL INTEGUMENTS.

The question of the duality of the Cycadean and other amphivascular testal structures has received only incidental mention while commenting on the homogeneous development of the *Bowenia* ovule observed by Kershaw (1912). But it has been assumed that the *Lagenostoma* cupule is a very significant structure and that an amphivascular condition must quite invariably indicate duality of origin; that is, lateral fusion of the members of two successive whorls with subsequent more or less complete radial fusion of these. So far as recalled, Stopes (1904, 1905) was the first to suggest that the cycad testa is essentially double, a view others have been cautious about accepting. Scott (1909) and Coulter and Chamberlain (1910) express doubt, and earlier, in Volume I, page 234, the compact form of mention given the Cycadeoid and *Lagenostoma* integuments includes no definite conclusion as to the final homologies involved. Recently Salisbury (1914) infers that duality of the integument in Cycads is unlikely because of the homogeneous development in *Bowenia*, and more especially the anatomy of the Paleozoic *Trigonocarpus shorensis*, in which such inner flesh as is present is simply an unsclerized internal lining of the hard shell facing the free nucellus.

Certainly the typically monovascular *T. shorensis* seed may never have been amphivascular. However pertinent is the evidence afforded by this ancient seed, no general theory can be founded upon it alone, and it must be admitted that the idea of an extensive testal duality is by far the more conservative. Both lateral and radial fusion so commonly occur in floral organs that there is not the slightest necessity to assume that traces of a fusion line between two seed envelopes developed in the old Paleozoic would be evident in even the earliest growth stages of present-day seeds. Since in the ancient gymnosperm seeds the nucellus is so often free and there are so many forms with the apical complication of the endovascular integument and free cupules, while other and striking forms are distinctly extravascular and with or without cupules, the conclusion is clear that several series of protecting whorls took part in testal evolution. Furthermore, in just such envelopes one begins to see the prototypes of calices and corollas. But whether or not, as will presently be maintained, megaspore coats or testas are analogous to and were the actual prelude to floral envelopes, it is probable that even in the case of the better-known ancient seeds there was not an entire uniformity of testal origin. We are too prone to hypothesize along linear instead of successive horizontal lines. Even more distinctly in Devonian time than later evolution was a frontal, a zonal movement dependent on geologic periodicity and involving countless forms, changing now in one set, again in another set of organs. In short, the one safe assumption is that the protective layers discernible in the ancient seeds did not arise at precisely the same time and were not subject to the same course of either development

or reduction; and while the development of the testa as a whole can so largely be accounted for as a process of reduction, the one feature strictly progressive and persistent was the sclerenchyma layer which always became the fixed or zero point on either side of which lay the great region of change. That subsequently to the establishment of a sclerous layer either endovascular or extravascular bundle systems ever arose is not believable.

POLYPHYLY.

If the foregoing views are in the main correct it is not necessary to assume a uniform derivation of dimerous from trimerous or hexamerous seeds, however readily transitions between these types may be conceived to have occurred. The more facile conception is that the several types arose in closely related forms as the result of the same impulse. In fact, variations from the norm appear to have the nature of sports or saltations, and the seed angles, once established, seem to have strongly tended to persistence throughout all subsequent changes down to the present day, as witness these observations by Salisbury, who, however, would hypothesize hexamerous prototypes (1914, p. 70):

"A striking feature of the Trigonocarpeæ is not only the occurrence throughout of the hexamerous type, but also the absence of variation in the individual species. This stereotyped character suggests analogy with present-day Monocotyledons, and is in marked contrast to the variability exhibited by the Lagenostomales, not only as between different genera and species, but also as between individuals. For example, in *Physostoma* nearly 50 per cent of the seeds had 10 ribs, but the remainder exhibited from 9 to 12. In *Conostoma* the number was 6 or 8 according to the species, with one recorded variant of *Conostoma oblongum* possessing 7. In *Lagenostoma Lomaxi* the normal number was 9, and for *L. ovoides* 8, with variation from 6 to 9. Finally, in *Gnetopsis elliptica* the number of ribs was 4, with perhaps 2 others vestigial. In this series we see that there is almost every variation from 4 up to 12, and while a multiple of 3 is by no means infrequent—a reminiscence perhaps of relationship to the Trigonocarpeæ—the more normal feature is some multiple of 2.

"Our knowledge of the structure of *Conostoma* and *Gnetopsis* has shown how narrow is the dividing line between radiospermy and platyspermy. Also the recent discoveries of *Aneimites fertilis* (1904) and *Pecopteris Pluckeneti*, together with the obvious relations between the Pteridosperms and the Cordaiteæ, render it necessary to consider the possibility of deriving bilateral forms from trigonous groups. The fact that the (dimerous) fructification *Pecopteris Pluckeneti* was borne on a Medullosean type of foliage certainly indicates such a change, so that the analogy afforded by examples from the carpellary structures of the present-day flora may not be without value. The *Carices* are represented in the British flora by about 50 species, of which over 30 possess 3 stigmas associated with a triangular nutlet; the remaining species mostly have 2 stigmas, and the nut is either bilaterally symmetrical or plano-convex. In a few species with two stigmas the nut is slightly trigonous, and in *Carex paludosa* Good., the stigmas vary from 3 to 2, accompanying which the nut is either trigonous or lenticular.

"As an example from the Dicotyledonous series, the Polygonaceæ furnish us with a group in which triangular fruits are the rule. In part of the genus *Polygonum*, and in the genus *Rumex*, a triangular nut is associated with 3 stigmas. In the section *Persicaria* of the genus *Polygonum*, and in *Oxyria*, the fruit is lenticular and composed of only 2 carpels, as shown by the pair of stigmas.

"To come much nearer, the fructifications of *Ginkgo biloba* have been found with 3 ribs in place of 2, a variation that may even be a reversion.

"In view of the frequent association in the monocotyledonous series of trimerous flowers with a triangular stem structure, an expression probably of similar mechanical relations, it is of interest to note that the general outline of the stems both of *Medullosa anglica* and *Sutcliffia insignis* was broadly triangular, though the character does not of course hold for other species of the former genus."

The fossil record indicates that seed types may persist throughout very long periods of time. In certain groups the characters are fixed; in certain others they vary within minor limits, the type persisting as a variable one. The observation by Salisbury of *Ginkgo biloba*

seeds with three ribs in place of two may very well indicate older relationships. Trigonous seed casts in the Yale collection of Permian plants from the ironstone nodules of Mazon Creek (Illinois) are quite worthy of note in this connection. These casts are readily removable from their matrix and exhibit a very unusual beauty of conservation; even the original whitish color persists and it seems extraordinary to find that mineralization could thus simulate the appearance and color of recent seeds in forms so ancient. In fact, size, color, and texture are so like that seen in *Ginkgo* that, except for the additional angle, these seeds would readily be taken for typical Ginkgoalean types. With respect to the dicotyledonous seed series it is quite as reasonable to ascribe polyphyly and ancient origin as in gymnosperms. Entirely too much has been made of the idea of a recent origin of dicotyls. Stopes has recently shown the presence of five new genera of typical dicotyledonous woods in the Lower Cretaceous, and it is certain that diversity of wood structure in the dicotyledonous lines is still vastly older. There is nothing in the way of hypothesizing the presence of essentially modern types of dicotyls in the earliest Mesozoic.

It is fairly safe to conclude that from no point of view does it now seem possible to explain seed ribs as in any proximate sense of directly mechanical or utilitarian origin, however much the testa as a whole may be so regarded. Although the extent to which morphologic interest rather than taxonomic value should be ascribed to radiospermic and platyspermic series must in many cases long remain in doubt, this is mainly owing to the paucity of the fossil record. Taken in entirety, however, this record already answers the main question as to whether or not the basis for the diversity seen in seed and even in modern floral types had already been laid down in the early Paleozoic. The platyspermic seed series so beautifully illustrated by Brongniart (1874), *Cardiocarpus*, *Leptocaryon*, *Rhabdocarpus*, *Sarcotaxus*, *Diplotesta*, all unite with the triradiate *Pachytesta* and numerous Trigonocarpons to form a most impressive series; and of the direct continuation of this series by the 5- and 6-ribbed seeds as mostly demonstrated from the "coal ball" types and again seen in the Cycadeoideæ, there can be no doubt. But taking all the known forms together, however much homogeneity of origin they may have stamped upon them, it is easier to conceive of the main lines of advance leading towards multiplicity of type as having been securely established in very early geologic time. Even in the entire absence of any other evidence than that directly afforded by ancient testal structures, it would be necessary to ascribe complexity of origin to the Paleozoic gymnosperm seed series. But there is also the collateral testimony yielded by the seed-like *Codonotheca* and the staminate disk of *Cycadeoidea*, first forming single cupules. These may indicate an early composition of seed coats from sterile or sterilized leaves with a resultant possibility of many and striking mutations. However, it is more convenient to relegate the consideration of this advanced and much more distinctly speculative phase of seed origins to the separate succeeding topic. So doing makes it practicable to limit the present descriptions and discussions to the Cycadeoid seed taken as one of the most generalized of gymnospermous types, which despite the retention of pronounced Cycadofilicalean features may yet be included amongst the Cycadales. And, while leaving classifications to evolve themselves as they may, it has been most interesting to observe that not only were the primitive seed characters of the Cycadeoideæ little obscured by appression in the peculiar strobilar type so much affected by the group throughout the Mesozoic, but even so much the more surely conserved as to permit the freest comparison with the ancestral singly-borne multilobate leafy seeds of Paleozoic times.

HYPOTHETIC RELATION OF SEED TO FLOWER.

Before leaving the subject of Cycadeoid seeds it seems very desirable to take up several hypothetic rather than theoretic conceptions of a possible and indeed probable far-reaching relationship or essential homology between testal structures, cupules, staminate disks, and floral envelopes. Botanists have come to understand very clearly, within the past score or so of years, that following the development of heterospory megaspore retention was the second and megaspore protection the third great stage in the evolution of early seed plants. This general subject has been discussed with clarity by Coulter among others; but to what degree sterilization has played a part in the development of testal structures still remains unknown ground; and that there may be some very direct relationship between testal structures and floral envelopes is a possibility hitherto so little considered that in the discussion which follows many points must be left obscure.

There are, of course, several well-defended theories and conceptions of what the general course of plant and animal development has been like. A few years ago the general tendency was to represent the course of change as one of constantly increasing complexity, but latterly there is somewhat less inclination to insist on the idea of a continual dichotomy with the sending out of vast numbers of lines or races destined to become extinct, for it is now found that the net result of paleontologic discovery is to throw origins of present-day types farther and farther back. As a consequence, it is already obvious that there has been a much greater parallelism and homoplasy in the development of modern types than was once thought possible. In this connection the thesis of Steinmann (314) should be especially mentioned to the effect that past mutations have been very great and that in the course of time relatively few of the races of animals and plants have wholly disappeared; in short, that reductions have played a great rôle, devolutions being in a very large measure responsible for the obscurity of relationship and difficulty of classification encountered so often. The fact, too, that the course of geologic change has been periodic and that climates have always been zonal must be held firmly in mind by botanists.

But at the same time the gaps in the fossil record run by whole geologic periods, and it is obvious that relative abundance is not an aid in establishing "missing links;" for while some of the better or less known fossils must stand in the directly ancestral line, the number of such must be exceedingly small, it being almost invariably the specialized and nonplastic races which are most in evidence. So true is this that ideas of what constitutes primitiveness have to be continually reconstructed. In fact, nowhere else than just among the existing cycads and conifers is it more difficult to separate primitive members from those which are in a high degree specialized and terminal. On a later page it will be briefly shown how opinions have differed as to which are the older conifers and how there is nothing that can be cited from the results of recent years showing that conifers and most Cycads—Gnetaleans are more debatable—can be viewed as Angiosperm ancestors. Here it is rather the purpose to lay stress upon the idea of frontal movements in evolution and in particular to suggest that conifers and most cyads have long been separated from dicotyls, and that when seeds with little-reduced coats were being organized into cones, other forms, the true dicotyl ancestors, with simpler testal structures, adopted the flower habit. In particular, it is wished to point out that sterilization may have played a great rôle in megaspore protection as well as origin and that there appears to be a definite analogy between the gymnosperm seed coat and ancient disks. Meanwhile, the critic must recognize that what is said is the simplest attempt possible to bring into closer view some of the hypotheses of seed and floral structure suggested by the fossil structures in hand. True enough, the Cycadeoid seed coat

in itself offers no evidence for either direct or indirect origin of seed coats; and taking the seed itself, all that can be said of it is that, more than any other mesozoic form known, it retains old features, although simple enough in structure to permit comparison with conifer rather than present-day cycad seeds. But the fact can not be summarily dismissed that in *Tumboa* the disk incloses an aborted and perchance primitive type of megaspore, while in *Cycadeoidea* there is a disk dome as distinctly tentacled as is the canopy of ancient seeds. If ever such disks were hypogynous to primitive types of megaspores, a possibility at once suggested by the microspore-bearing disk *Codonotheca*, the lobes might well have closed in to form more or less complex testal envelopes differing but little from ancient seed coats. Moreover, if, as there is excellent reason to believe, various types of disks anciently existed, it is by implication much easier to understand how manifold floral types arose. Before taking up this far-reaching hypothesis in the discursive manner which is alone possible at present, it is very desirable to consider at some length the alternative or synangial conception of testal structure.

THE SYNANGIAL HYPOTHESIS OF TESTAL ORIGIN.

More definitely and clearly than any one else, Miss (Professor) Benson has hypothesized the direct evolution of the seed with its complex testa from "a synangium in which the peripheral sporangia are sterilized and specialized as an inner integument." In Volume I (p. 124) the idea that gymnosperm seeds are giant spores inclosed in an integument derived from an indusium or a synangial wall of Marattiaceous type was inadvertently referred to Engler. It is justly that of Miss Benson (1904), for whose elaboration (together with Figure 58) space may well be accorded:

"The seed *Lagenostoma* (the three species of which were first named and partially described by Williamson) has since received a searching investigation at the hands of Prof. F. W. Oliver. The connection of one species, *L. Lomaxi*, with *Lyginodendron* has recently been announced by him and Dr. Scott. To quote from their account of this species:

" 'In the most general relations of its organization the seed approaches the Gymnosperm type in that the integument and nucellus are distinct from one another in the apical region only, whilst the body of the seed which contains the large single macrospore shows complete fusion of the integument and nucellar tissues. But in other respects the seed is remarkable. The integument, which is a simple shell where fused with the nucellus, becomes massive and complicated in its free part which corresponds to the upper fifth of the seed. In this region it is usually composed of nine chambers radially disposed around the micropyle. The whole structure from within is like a fluted dome or canopy, the convexities of which correspond to the chambers. The vascular system of the seed enters as a single supply bundle at the chalazal papilla and branches a little below the base of the macrospore into nine radially-running bundles. Each of these bundles passes without further branching to the apex of the seed, running outside the macrospore and a little distance below the surface. At the canopy the bundles enter the chambers and end at the tips.' [See text-fig. 60.]

"A somewhat lengthy quotation has been made, as it is necessary to understand the structure of the seed if the comparison with the microsporangial sorus is to be appreciated. The transverse section of the seed, if taken in the plane of the canopy, somewhat resembles a cartwheel, in which the nucellar apex forms the axle, the radial walls between the chambers the spokes, and the peripheral walls of the chambers the rim of the wheel. The comparison does not hold good, however, in well-preserved sections, as the chambers are seen each to contain large, thin-walled cells which support the delicate branch of the vascular bundle that is contributed to each.

"The correspondence which must have already suggested itself to the reader is between such a seed as *Lagenostoma* and such a synangium as *Telangium Scotti*. The chambers surrounding the nucellus seem to represent its sister sporangia, which have become sterile, the large-celled, thin-walled tissue and delicate vascular strand being all that represents the ancestral sporogenous tissue; while the micropyle corresponds with the original space between the tips of the sporangia. The

seed, in fact, is assumed to be a synangium in which all but one of the sporangia are sterile and form an integument to the one fertile sporange which has become a megasporange with one large megaspore. In *Lagenostoma physoides* the integumental ridges are continued into tapering tentacles around the micropyle, and this still further accentuates the resemblance to a sorus. In *L. ovoides* the number of chambers is often seven instead of nine. Hence we have only to imagine that one of the sporangia of a sorus of eight or ten sporangia gradually evolved megaspory, and that the remaining seven or nine sporangia became a sterile envelope—a correlation in development which has many analogies in the animal and vegetable kingdoms. As soon as one of the sporangia became a

FIG. 58.—*Telangium Scotti* Benson. After Benson.

Supposed microsporangiate fructification of *Lyginodendron*. Longitudinal and serial transverse sections of synangium, with restoration and comparison with *Lagenostoma*.

1, 8, longitudinal synangial sections, 1 traversing two adjacent synangia with apical region S of fusiform cells sclariform walled; 2–5, 7, various transverse sections passing from fused basal region to the level of discrete sporangial apices (2–5, ×15 to 20; 7, ×4); 6, spores of *Telangium* (above) with pollen-chamber spores of *Lagenostoma* (below) ×100; 9, comparison of apical region of synangium with toothed region of *Lagenostoma*, enlarged; 11, *Calymmatotheca Stangeri*, ×½; 12, *Telangium affine*, ×2; 10, *Telangium* restoration, ×2.

megasporange the symmetrical arrangement of the sister sporangia would become an advantage and naturally follow. At the remote period of time at which the seed was evolved, a period probably anterior to the Carboniferous epoch, it may be conjectured that the arrangement of the sporangia in the sorus was irregular, and that the more centrally placed sporange with its better vascular supply may have gradually attained the megasporangial condition. In *Gleichenia* and *Oligocarpia* some sori have, and others have not, a central sporange. As respects the vascular supply in the center of each compartment of the integument, it is well known that in many of the Permo-Carboniferous seeds a vascular bundle entered the base of the nucellus, even passing from the chalaza to the pollen chamber, and it is hence easy to conceive of a vascular strand having early entered its sister sporangia. Again, if we take an example from a seed of very remote affinity, we find that in *Castanea* a vascular strand may be demonstrated running up the whole length of the nucellus, and is especially well developed in nucelli whose embryo-sacs have long remained unfertilized.

"I will now proceed to show that this interpretation of the integument of *Lagenostoma* is helpful in clearing away many of the difficulties that have beset the general problem of the integument hitherto. The more generally accepted interpretation of the inner integument is that it is due to a special development of the indusium. We are compelled to regard the integument of *Lagenostoma* as a single integument, firstly because of the primitive character of the seed, and secondly because of the existence in *L. Lomaxi* of an exterior envelope. Hence it is probably safe to regard it as homologous with the inner integument, and consequently as hitherto accounted for merely by Celakovsky's theory of the indusium, or by another theory to which I will allude later. But the cohesion of integument and nucellus which we know to be characteristic of the Cycadean seed receives no explanation on the indusial theory, whereas on the synangial theory the cohesion is seen to be due to the origin of the seed from structures already coherent.

"Moreover, as it is generally agreed that the heterosporous habit arose from the homosporous, it is *a priori* probable that there should be a correspondence between the microsporangial sorus and the primitive seed, and this correspondence seems best obtained by harmonizing the seed and the synangium.

"If it should be shown conclusively that *T. Scotti* is the microsporangial organ of *Lyginodendron*, the homologizing of *Lagenostoma* with its synangium would simplify the problem of the integument in that we should then have but one envelope to account for in the seed over and above what was present in the male sorus.

"I will now refer shortly to another widely accepted view, which has been adopted by Strasburger, Treub, and Dr. Lang. Though their views vary as to the homologies of the seed as a whole, they agree in regarding the integument as a new formation.

"Dr. Lang's conclusions are based on his own investigation into the morphology of the sporangia of *Stangeria* and on the results of work by Warming and Treub on other genera of Cycadaceæ. He points out that 'with regard to the development considerable correspondence between the ovule and the sorus can be traced in the early stages. The differences between the development of the sorus of microsporangia and the ovule only became pronounced when active growth becomes localized around each archesporial group.' He therefore homologizes the sorus and the ovule at the outset, but looks upon the ovular sorus as monosporangiate and the integument 'as an annular upgrowth, around the apex of the nucellus, of the bulky sporangial wall or, which comes to the same thing, of the edge of the receptacle which had kept pace with the single sporangium.'

"Thus it would appear that owing to the relatively advanced type of seed investigated, Dr. Lang could not homologize the upgrowing 'edge' of the receptacle with sterilized sister-sporangia of the nucellus. He adds that his view is only put forward as a provisional statement, which will have to be tested 'in the light of the evidence obtainable from extinct forms.' It is in the light of these extinct forms that the new theory of the integument is now being put forward.

"Whether *T. Scotti* be ultimately proved to belong to *Lyginodendron* or not, we may well bear in mind that the synangium is a very ancient type of fern fructification, for from the Culm onwards we have numerous examples of it recorded. Where the individual sporangia are not entirely coherent they generally form a sorus of bulky sporangia like those of the Filicinean class 'Simplices' suggested by Professor Bower. The ancient sporange was very rarely solitary, and we have already undoubted evidence in *Cycadeoidea* of a seed-plant having synangia for its microsporangial organ.

"Among synangia which are found to be associated with Cycadofilicinean seeds are *Hawlea* and *Scolecopteris*. The latter I will shortly describe, as I believe a reference to it may make the comparison of seed and synangium more clear. *Scolecopteris* is a form-genus including several species of sorus, which have been described by a succession of paleobotanists. It is sufficient for our purpose to refer to the drawings of *Scolecopteris polymorpha* in Engler and Prantl, Teil I, Abt. 4, p. 440. It will be seen that the sorus, as a whole, somewhat resembles *T. Scotti*, but the four or five sporangia, which here constitute the sorus, are inserted around a pedicel along which runs a vascular strand. If this were to become continuous with a strand of tracheides developed in the sporogenous tissue, we should obtain the vascular supply which characterizes *Lagenostoma*.

"The beautiful plates in Brongniart's *Recherches sur les graines fossiles silicifiées* (1881) afford many opportunities of applying and testing the new theory, and amongst others I would suggest a reference to the following: Plate IX, Figure 4, showing a vascular bundle entering the nucellus in *Rhabdocarpus subtunicatus;* Plate XIII, Figures 6, 7, 17, 19, showing the contrasted tissue-systems of the integument of *Sarcotaxus avellana* and its septicidal dehiscence; Plate IV, Figures 1 and 3, showing the spor-

angial appearance of the inner integument continued to the base of the nucellus in *Cyclocarpus nummularis*. (These figures should be compared with *Telangium Scotti*, Fig. 58.) See also Brongniart's Plate C, Figure 9, in which the seed *Codonospermum* is shown to present a striking resemblance to such a synangium as *Asterotheca*.

"The similarity of the inner integument of *Pachytesta* to that of *Lagenostoma* has been recently pointed out by Professor Oliver and a transverse section has been constructed which exhibits its compartmental nature at a level much lower than that in which it can be demonstrated in *Lagenostoma*. Professor Oliver adds: 'The presence of vascular strands in the chambers of *Lagenostoma* is the most important difference.'

"Much fuller details are to hand of another seed which seems to bear out this theory. I refer to *Bennettites Morièrei*, Sap. and Mar. (spec.), which has been admirably worked out by Professor Lignier (1894). This fructification, as is well known, belongs to a much later horizon, *i. e.*, Mesozoic, and shows Cycadean affinities. If one consults Lignier's Plate III, Figures 35 and 37, one sees transverse sections of the upper part of the seed, showing the thick integument divided up into four compartments by radiating vertical walls of flattened cells, very comparable to those which separate the constituent members of a synangium.

"The interior of each compartment is described as succulent tissue, but offers an abrupt contrast to the walls. Plate III, Figure 38, shows the constitution of the integument at a lower level. Here we find the peripheral epidermis of the integument lined, as in *Telangium* and other synangia, with a layer of reticulately thickened cells within which lie the large thin-walled cells which seem to correspond with the sporogenous tissue, and this is limited internally by thick-walled fibers. Plate IV, Figure 45, shows also on a smaller scale the compartmental structure of the integument.

"It is interesting to note that *Bennettites Morièrei* is in some respects evidently less reduced than *Bennettites Gibsonianus*, in which, as Dr. Scott says in his *Studies*, the structure of the pericarp is a matter of inference. Nor is there any possibility of avoiding the conclusion that the inner tube of the micropyle is nucellar in origin if we accept the diagrams Professor Lignier gives.

"I can not but regard this example as very strongly confirmatory of the homology of the seed with the synangium. If we compare the peripheral epidermis of the integument with that of the microsporangial sorus of *Cycadeoidea* we obtain a possible explanation of the radially elongated epidermal cells of the sunken seed. Is it possible to call in here the aid of a wholly hypothetical indusium and invest it in turn with so many points of similarity to the sister sporangia of the nucellus, sporangia which it can not be granted originally surrounded the ancestor of the megasporange? Or, on the other hand, can we, with others, call in a new formation to account for an integument so obviously compartmental?

"Thirdly, I wish to refer to the seeds which somewhat unfortunately go by the name of *Gnetopsis elliptica*, Ren. Although they are not yet worked out with the same detail as *Lagenostoma* and *Bennettites Morièrei* there is considerable internal evidence in support of their synangial origin. They are figured (after Saporta and Marion) in the English edition of Solms-Laubach's Fossil Botany, on page 128, and come from the Upper Coal Measures of Grand' Croix. The ovules occur in one or more pairs in the hollow of a cup-like envelope which bears long hairs.

"For convenience I will quote from Solms-Laubach's description of this most interesting type:

"'That portion of the integument which incloses the apex of the nucellus behaves in a very peculiar manner, and may be compared with *Lagenostoma*, Will. It attains a considerable thickness and separates into a compact outer lamina (canopy?) and a similar inner lamina, while the cell-layer between the two is formed of extended filaments which represent so many cells and traverse a broad intercellular space at some distance from each other. This looser tissue ceases, of course, at the micropylar canal, where the outer and inner layer are in connection with one another. Th margin also of the orifice of the micropyle is formed of a cup-shaped expansion which is seen to be drawn out at two points into long filiform appendages. A vascular bundle enters at the base of the ovule and splits into four branches.'

"If this account were translated into the language of this new theory we should say that each of the four abortive integumental sporangia contains loose elongated cells in its upper part, and that their extreme apices are prolonged much as in *Lagenostoma physoides*, only that they remain adherent in pairs. The other two species of *Gnetopsis*, *G. trigona* and *G. hexagona*, are known only as impressions, and show four or five tentacles around the apex.

"If it should be contended that in the case of *Lagenostoma* and *Gnetopsis* this special development of the inner integument is merely of biological significance, I would point out that it is difficult to see, then, why this should also occur in a seed outtopped by interseminal bracts, as *e. g.*, *Bennettites Morièrei*. Nor does this explain the form of the section of the seed—triangular, hexagonal, etc.—nor the radiating vertical walls dividing the integument into compartments.

"If, however, such internal evidence as I have brought forward appears inconclusive, it is satisfactory to find that there is a record in the literature of an exactly comparable transformation occurring in the sorus of a very ancient monostelic fern stock. I refer to the fact that Renault, in his Autun Flora, describes a specimen of *Botryopteris* sporangia in which a group was found to be surrounded by an envelope formed of *sterile and highly modified sporangia*. Renault figures some of these sterile sporangia in his *Flore fossile d'Autun et d'Épinac*.

"When we consider that on anatomical grounds it has long seemed probable that the Cycadofilices arose from some ancestral Filicinean group such as the Botryopterideæ, we see that such a case as Renault cites is peculiarly significant in any discussion as to the phylogenetic origin of the integument of the seed. Hence any further confirmation of Renault's observation would lend a strong support to the new theory.

"I will now refer to a few analogous cases which lend a general support to the claim for the sterilization of certain sporangia in a sorus during the evolution of the seed. In *Azolla* I believe most morphologists would admit that the microsporangial and megasporangial sori were originally similar, and that the megasporangium has gradually lost by abortion a number of sporangia, retaining only one. If the developemnt of the megasporangia in *Azolla* involved the total loss of its free sister sporangia, are we claiming too much if we conjecture that in another fern the sister sporangia, which were already adherent, were retained as a sterile envelope?

"Turning to the Angiosperms, the modification and abortion of flowers in an inflorescence to construct the biologically interesting "flag apparatus" is exceedingly common. The peripheral flowers in the capitulum of the *Cynareæ*, in the thyrsus of *Viburnum opulus* and *Hydrangea*, are among the most familiar examples. In *Muscari comosum* (var. *racemosissimum*) a very remarkable modification follows the sterilization of the central flowers. In *Rhus cotinus* De Candolle noted an increased growth of trichomes on the pedicels of the sterile flowers, and it has hence become a classical example of what he meant by the expression 'correlation of growth.' Passing from flower to sporophyll we have no need to mention any of the innumerable instances of the change from stamen to sheathing organ which occurs commonly in Ranunculaceæ, Scatimineæ, etc. In *Salvia* we find that half the anther is sterilized to provide the lever which is to assist in the process of cross fertilization. If a part of a sporophyll can be sterilized and adapted for an accessory function, why should not some members of a synangium?"

However insufficient the foregoing hypothesis of synangial sterilization as the basis of seed origin may prove with time, and time alone can test it, how little the structure of *Gnetopsis* or the passage from stamen to sheathing organ supports it, is hardly to the point. The long quotation in any case serves admirably to bring into full perspective some of the most important elements in this central problem. Certainly it would be very difficult to sustain the idea of some very direct evolution of the gymnosperm integument as a new structure because of the complex apex. In fact, it is probable that any such attempt would lead back finally to some of the views earlier held by the French paleobotanists who attached so much importance to the highly organized stem structure of the Calamites, Lepidodendrons, and Sigillarias. As now so well known, the seed-like organs developed by some of these forms must have functioned as seeds in much the same sense as those of Cycadofilicaleans, although, as Dr. Scott remarks, greatly inferior to the latter in morphological differentiation and much nearer the Cryptogamic type of megasporangium. Since, as Dr. Scott adds, "the Lepidocarpons are the only really primitive seeds known," it is easy to see that the morphologist can make little headway in his attempts to account for so striking and complex structures as the early seed coats without the aid of some kind of extensive mutation and change of function in organs leafy or otherwise already present.

Unquestionably one of the greatest stumbling-blocks in the way of the synangial theory is the sporangial grouping. Spirally inserted organs readily reach circular emplacement as closed whorls, but it seems very difficult to derive a symmetrical lobed seed from the fusion of seven or eight sterile synangia about a more or less eccentric megasporangium. Everyone who has ever attempted to hypothezise courses of change in ancient plants realizes most keenly that the very moment asymmetry is invoked or in the slightest degree ignored, even the old and familiar milestones become obscure. If the nine or ten *Lagenostoma* canopy divisions were really well-marked chambers, derivation from the Crossothecan, or (as Miss Benson suggests) some much simpler synangial type, would be a step easier. Mark well, however, that *chambers* are not present, but simply bundle-supplied divisions, interior to which is the lagenostome likewise best explained as segmental in origin. For all practical needs of comparison one gets just as far by taking a very reduced (?) seed like *Sphærostoma*, where there is no chambering due to deceptive conservation and less "intercalated" structure.

FIG. 59.—*Mittagia seminiformis* Lignier. ×12.

Westphalian "coal ball" megasporangia of unknown attribution. Longitudinal section traversing two adjacent megasporangia at point of attachment. Four megaspores are normally present in each megasporangium. From Lignier (1913).

1–4, megaspores, of which Nos. 1, 4 only are cut in median plane; *c*, palisaded outer layer; *p*, parenchyma layer; *n*, lamella or membrane interior to parenchyma of megasporangial coat; *e*, exine; *m*, metine; *i*, intine of megaspore; *b*, protoplasmic spore content.

The plain fact is that the synangial theory not only fails to account for the finely developed cupules present in both *Lagenostoma* and *Sphærostoma*, but involves the outright evolution of almost the entire lagenostome region in a manner difficult to comprehend; while it must be confessed that, after all, the bearing of about the only example of the heterosporous condition attributable to a Crossothecan relationship, so far noted, is quite obscure. Dr. Scott observes that in the same petrifications yielding *Telangium*, bisporangiate synangia which can not be readily separated from *Crossotheca* are found, with the additional complication that each sporangium is subdivided into two loculi. This, of course, adds nothing, and perhaps the testimony as to the nature of ancient megasporangia afforded by the notably interesting fossil *Mittagia seminiformis* (Fig. 59), recently described by Professor Lignier (1913), from the Westphalian coal balls of Austrian Silesia, is even negative; for in *Mittagia*, which resembles *Lagenostoma* in size and outer form as well as in the palisaded sclerenchyma, but is without apical lobes or bundles, four megaspores are present without the slightest trace of elongation; nor is it conceivable that with sterilization to a single megaspore any marked apical changes would have been produced. Of course, *Mittagia* is a sporangium, and it would be markedly easier to conceive it as having arisen from a course of synangial sterilization than it is to believe that *Lagenostoma* was so produced.

The discussion of the synangial hypothesis, either *pro* or *con*, is difficult to carry much further forward at the present time, and it appears quite likely that the main prerequisite to further progress in this direction is the accumulation of new fossil evidence rather than

the regrouping of old facts; but whatever the outcome, it is very interesting to recall that easily the most striking feature evident in the staminate fructification of *Cycadeoidea* when first discovered in 1899 was the close resemblance of the sori to the fruits of carboniferous ferns of Marattiaceous type, the essentially staminate character of many of which was then unknown, although definitely suspected; while it was but little more than a year later that a fairly adequate discussion of the Cycadeoid synangium was given in which it was definitely predicted that the Crossothecan synangia would eventually be found accompanied by seeds. Moreover, it was pointed out that the facts brought together by Bower, in his superb monograph on the *Morphology of Spore-producing Members*, taken with such fossil evidence as could readily be cited, indicated a great antiquity for all synangial types. Up to this point speculation certainly went hand in hand with the progress of discovery; for it was but a very short while until Scott was enabled to take the obvious view, following proof of the seed-bearing nature of *Lyginodendron*, that the Marattiaceæ and Pteridospermeæ may have owed their synangic fructifications to some common descent from a primitive group of Filicales in which that character had already appeared. That the discrete pollen sacks of *Ginkgo* and the *Angiopteris*-like sorus of recent cycads are less readily explicable as synangial derivatives must be admitted, this being the principal contention earlier advanced (378, p. 433) which now seems debatable. All in all, however liable to a dual interpretation may be certain of the facts cited in the foregoing pages, it can scarcely seem to the discerning botanist that too great prominence has been accorded by anyone to the Crossothecan synangial type.

THE DISK HYPOTHESIS OF TESTAL ORIGIN.

That the synangial hypothesis is not the sole possible means of accounting for the complex structure of ancient seed coats is a very recent observation resulting from the discovery of the eared or diceratoid character of the staminate fronds of *Cycadeoidea* so far only seen to advantage in *C. colossalis*, but doubtless present in most if not all of the silicified forms. This remarkable and for long quite unsuspected feature is described under the heading *Cycadeoidea colossalis*, and as the preliminary interpretation (1914) remains without any sufficiently definite criticism, it may best be repeated here without essential change:

For several years past it has been very strongly suspected that modified disks must have played a prominent part in the origin of diversified floral types, but it was scarcely understood that a theory of the seed should also involve floral structure. As a consequence, the diceratoid disks being unknown, the inherent difficulty of formulating some kind of rational flower hypothesis, as attempted in a contribution to the Botanical Gazette, was greatly increased. The disks as now understood suggest highly interesting modifications of the hypothetical figures then given which anyone seriously interested in these discussions may readily construct for himself. It does not seem sufficient to ascribe these peculiarly constructed disks to isolated instances of adaptation. As true flower-bud structures they certainly suggest a course of reduction from more megaphyllous forms connected with prefoliation as well as prefloration, and make it necessary to hypothesize great strobilar variety in that distant period when the early land plants, by means of simple stems and megaphylly, raised their crowns above the soil to make the world's first forests. No matter what interpretation is given to these flower buds, exteriorly so like various of the so-called *Neuropteris* seeds (Figs. 61, 62), they constitute evidence that fusion and emplacement of sporophylls coupled with reduction were notable factors in gymnosperm evolution, and point to an alternative hypothesis for the origin of the complex seed coats of early Paleozoic

time which no morphologist bent on making the fullest use of the paleontologic record can afford to ignore. They do suggest a means of simplifying our conception of the evolution of the early land forests; and they do go far to show how a great variety of floral structures could have been rapidly developed in late Silurian and earlier Devonian land plants, a variety permitting the evolution of later types of plants by a frontal or abreast course of development along more or less parallel lines. And certainly such a conception of the main course of plant evolution is more consonant with general facts of distribution and theories of climatic change than is any view of descent by a series of dichotomies.

There is, in short, a broad suggestion of parallelism and periodicity in plant evolution. It has hitherto been difficult to reconcile the meager record of Silurian plants with the sudden appearance of varied Devonian types well advanced and so persistently lacking in forerunners. But this paucity of record is more easily accounted for if the direct evolution of new structures be held to have reached a climax in the first rapid covering of the land by homosporous types. From the leafy crowns of these earliest of all forest forms must in time have been derived the early heterosporous types, and from these in turn by continued sterilization emplacements, fusions, reduction and branching, a profusion of early seeds and then flowers. Such would be, hypothetically speaking, the line of least resistance in early plant evolution. We know that evolution of the early land plants may well have been rapid, just as many phyla of invertebrates develop diversity of form early in their history, and just as in recent geologic time, where islands have been freshly populated, plant forms elsewhere herbaceous quickly develop variety of species and tree-like stature.

That ancient seeds, then, have such a leafy structure appears to find the simplest explanation in the fact that a seed is as much a branch or derivation of a crown of fertile fronds as flowers have been conceived to be; and the striking character of the staminate disk of *Cycadeoidea* raises the question whether, in the sporophyll fusions and reductions resulting in seed coats, whorls of sterilized microsporophylls, or of bracts, may not in some forms be merged as seed-coat components, it being clearer now than ever that no one course of evolution can account for all the varied types of seed integuments. In some such manner the double nature of the integument in those forms where there is a series of inner testal bundles separated from an outer by the middle stone might be accounted for.

Finally, it is clear that if seed and flower have this dual homology and were thus successively derived from primitive homosporous crowns by one and the same general process of sterilization, fusion of leaves, and reduction, the relation of gymnospermous cones to angiospermous flowers can be more definitely defined than has hitherto been conceived possible. Especially, too, will it be seen that *Cycas* is in reality specialized and very closely apposed to other cycads when it is observed that instead of producing numerous compound branches or cones the seeds are simply distributed laterally along flat blades instead of spirally along cylindrical strobilar axes. Any known form which could qualify as an Angiosperm ancestor must therefore combine some of the characters of *Cycas* with those of *Cycadeoidea*, and this in a remote sense the Gnetaleans do.

EXPANSION OF THE CORNUTED DISK.

Before going on to consider the analogy between disk and seed-coat features, a word may be said about the expanded form of a flower like that of *Cycadeoidea colossalis*. So far, only the outline reconstructions of text-figures have been made, a more elaborate restoration awaiting study of further examples in somewhat better conservation. From the form of the flower and the inclosed position in which it grew, it is readily seen that it was much

easier for the disk to dehisce out of its close packing of bracts than to actually expand at the time of maturity; and as recalled from the description of other disks, the condition of the disk base usually found suggests that this was commonly the habit, although it is conceivable that forms existed in which the frond disk reached a large size and actually expanded.

If both pollen and ovules had reached maturity before the splitting away of the disk, close fertilization would have been facilitated to an extraordinary degree, provided only that there were free-swimming antherozoids, for without the intervention of these the outer surface of the ovulate zone would have remained shut off from pollination by the screen or mantle of decurved staminate frond tips. However, the quite immature condition of the ovulate region as compared with the stamens leaves in doubt both the time and mode of fertilization. The pollen may have undergone growth and development after shedding, several months even intervening before fertilization by motile antherozoids. Tison has described and beautifully illustrated the pollen-collecting droplets exuded by conifer ovules (343) and it is probable that such droplets were an aid to pollen-holding in the Cycadeoids, or also later contributed to the formation of a menstruum for the antherozoids. Lignier has suggested the possibility of parthenogenesis in *Cycadeoidea* (156), but there is no direct evidence indicating such a condition. Whatever value one may attach to comparison with other types of flowers is, however, secondary to the form and position of parts in the buds which are here alone considered with special regard to the reductions that might have gone on in similar but more ancient disks; and in considering questions of reduction it is very obvious that mere size is of a very secondary import. Also, throughout geologic time reductions have always been easily accomplished; nor is the absence of disk forms in the older formations any evidence whatever that such were not present in abundance from Devonian to Jurassic time in endless variety of form.

CORNUTED DISKS AND TENTACLED SEEDS.

What significance may be attached to the mid-ventral appendages of the cycadeoid disk? In the first place, it is difficult to know whether this structure is simply a result of growth response due to the appressed position of the bud and thus comparable to the thousand and one modifications seen in angiospermous flowers, or whether such disks are essentially ancient. Primarily the eared disk fulfils spatial and purely mechanical requirements in the isolated and far from representative side-line of the Cycadeoids in which it occurs. In fact, in the occasional *Williamsonia* flowers thus far observed no evidence of disk appendages has been noted. In the restoration of a Yorkshire coast disk by Hamshaw Thomas (331), Figure 81 D, it does appear that the frond tips were decurved, but ventral appendages remain unobserved if present. In the case of the reduced Oaxacan disk, appendages are likewise absent.

But whether the eared condition is primitive or not the vista of modification in Cycadeoid sporophylls is much enlarged; for even from purely mechanical considerations, it would seem very reasonable to suppose that similar disks must have characterized yet other primitive gymnosperm lines, and that such may shed some light on the origin of seed coats. With exactly this possibility in view the apical region of the flower bud may well be called a dome, which in reality it is, with direct thought of analogy to the "canopy" of the seeds of the Paleozoic Cycadofilicaleans. Moreover, if instead of a central cone one hypothesizes a somewhat reduced sterile-eared disk as inclosing a single giant spore, it is easy to see how the sterile tips of the fronds might be thrust forward so that if united edge to edge they must correspond to the lagenostome of the old gymnosperm seeds surrounded by ears or tentacles. The so-called lagenostome is variously developed in the older seeds, but in *Lageno-*

stoma, where its most typical form is seen, it rises as high as the outer elements of the "canopy." (See various text-figures.) Continuing, therefore, the analogy already suggested by the use of the terms dome and canopy for the outer apex of flower and seed, the staminate frond tips taken collectively are correctly named the *Cycadostome*. (*Cf.* Fig. 23.)

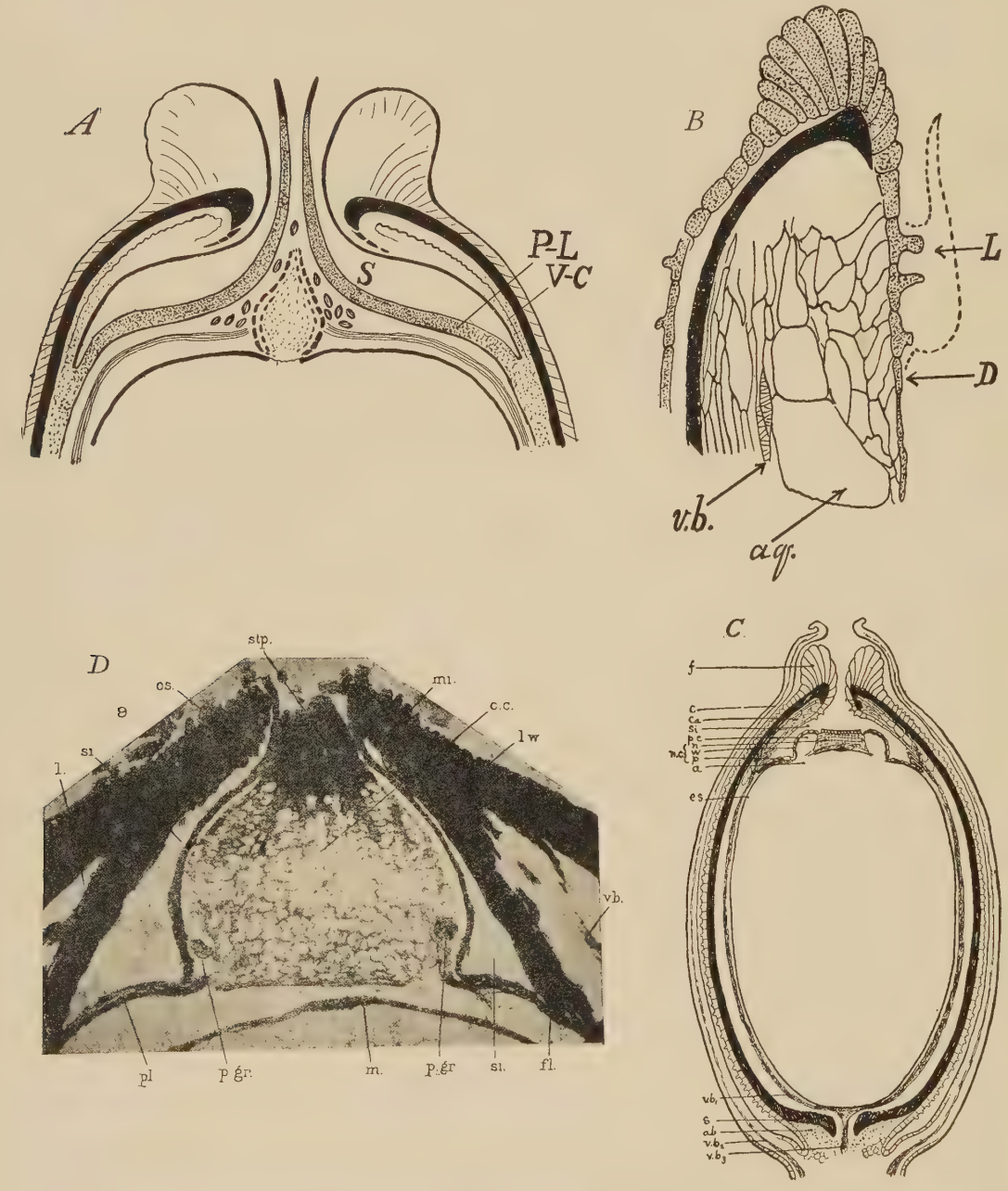


FIG. 60.—Composite seed type (A, B) suggested by *Sphærostoma* (C), and *Lagenstoma* (D). C, from Benson; D, from Prankerd.

A. Hypothetic seed: S, sinus; PL, plinth-lagenostome; VC, frilled canopy. B. Hypothetic *Sphærostoma*: L, position of exserted lagenostome; *aq*, aqueous tissue; *vb*, vascular bundle termination. C. *Sphærostoma ovale:* *f*, frill; *c*, cupule; *ca*, canopy; *si*, sinus; *pc*, pollen chamber; *n*, column; *w*, lagenostome; *p*, plinth; *a*, archegonium; *es*, embryo sac; *vb*, integument bundle; *ab*, abscission layer; vb_2, cupule bundle; vb_3, ovule bundle. D. *Lagenostoma ovoides:* *cc*, cancellated tissue; *stp*, stopper; *pgr*, pollen grain; *pl*, plinth; *si*, sinus; *os*, outer loculate wall; *l*, loculus; *vb*, vascular bundle; *m*, megaspore.

Whatever analogy there may be between disk and seed coat is made clearer by comparison of the hypothetic seed sections of Figure 60 with *Lagenostoma* and *Sphærostoma*. But it is first necessary to follow with care the details of the several figures. The longitudinal section A is that of a hypothetic seed. As drawn it is intended to suggest how the nucellar envelope might be formed by sterilization of a disk essentially like that of *Cycadeoidea colossalis*. Pollen grains indicate the chamber surrounding the micropylar "stopper." The wall of the pollen chamber is formed by exserted frond tips P–L, above which rise spurs traversed by vascular bundles V–C. Between the frond tips and the spurs is the sinus S usual to ancient seeds. The sclerotic sheath is in solid black. In the hypothetically modified canopy of *Sphærostoma ovale* (B), *vb* indicates the final traces of the vascular bundle supply of the canopy, *aq* an aqueous tissue, D the continuation of epidermal secretory cells, and L the possible plinth-lagenosome protrusion interior to a frilled dome. This figure is in every sense a repetition of A.

The seed *Sphærostoma ovale* (C) is quite exactly the size of a *Cycadeoidea* seed. In the longitudinal section of seed and cupule the sclerotic sheath is again shown in solid black. The elimination of the lagenostome is the striking feature in this seed otherwise comparable to *Lagenostoma*.

At D an especially good apical median longitudinal section of *Lagenostoma ovoides* is given 55 times the natural size. The micropylar opening is quite filled by a central cone or "stopper" of cancellated tissue *cc*, between which and the lagenstome wall *la* are several pollen grains *pg*. The sinus *si* is the space inclosed by the plinth *pl* and lagenostome, and the outer loculate wall *os*. The micropylar funnel would be formed by the inner faces of the spurs *os* if the lagenostome did not protrude.

The hypothesis advanced is that the polymerous testa of ancient seeds is essentially discoid and corresponds to the spurred staminate disk of *Cycadeoidea colossalis* less its fertile pinnules, the plinth-lagenostome consisting in a series of frond tips thrust forward interiorly to the canopy of spurs by megaspore growth.

On turning back to Figure 60 A, it should now be easy to imagine or construct the correspondent transverse sections showing the central frond tips forming the plinth-lagenostome region, and just half as numerous as the surrounding ceratoid ears of the hypothetic primitive frond components. Obviously enough, the same course of lateral fusion which results in the campanula would, if continued all the way to the frond tips, complete the inclosure of the megaspore; and this being the final object of such a process, it is quite unlikely that traces of the primitive lagenostome components would long remain, much less that such would in their inclosed condition fail of reduction. It is also plain that if such a process continued, suppression of some of the paired apical appendages might be the next change, so that a megaspore-covering made up of five or six fronds might soon show some variability from the normal number of ten or twelve tentacles; nor is it any more difficult to imagine this process of megaspore inclosure to go on in the case of a diad or triad than in the case of a tetrad or pentad of megaspore-inclosing fronds. Much more, in making these comparisons it should never for one moment be forgotten that angiospermous testal features are far simpler than those seen in the ancient gymnosperms and thus far more readily explicable as directly evolved features if any seeds can be so explained. Dimerous and trimerous seed coats are therefore no more complex than bilocular and trilocular pistillate flowers, the analogy between these structures probably being a deep-seated and far-reaching one suggesting that angiospermous flowers may be vastly more ancient than hitherto deemed possible.

MODIFICATIONS OF THE LAGENOSTOME REGION.

But before taking up any broader generalizations it is desirable to further test the disk hypothesis by briefly referring to much simpler types of seeds than *Lagenostoma*. For this purpose the *Sphærostoma ovale* from the Lower Carboniferous rocks of Pettycur, Fifeshire, Scotland, is one of the most interesting which could possibly be selected. As admirably described by Miss Benson (1914), this tetramerous seed is about 4 mm. in length and inclosed by a cupule which rises above and closely invests the extreme apex of the seed, finally dividing up into eight tentacles. Eight bundles, so nearly as can be determined, traverse the tissues of the cupule, which was probably fugacious; and as the inner flesh is also traversed by eight bundles, it may be assumed that testa and cupule both arise from the fusion of two alternant whorls of four or eight members each. Conformably the testa proper terminates in eight tufts constituting what Miss Benson terms the "frill," strictly comparable, however, to the tentacle or ceratoid outer appendages of other seeds. But easily the most noteworthy feature of this seed is the little-developed or very reduced character of the plinth tissues, which can scarcely be said to project forward into a distinct lagenostome and micropylar tube, as in other seeds of Carboniferous time. (See Figure 60 C.)

It is thus deeply interesting to find in *Sphærostoma* a lagenostome development so slight as to be barely traceable or else approaching obliteration, whereas in yet another thin-walled seed, *Physostoma elegans*, with a much less reduced but still comparatively simple testa, the structure of which has been elaborated with precision by Oliver, a small but distinct lagenostome is present. Now, lagenostome development is usually pronounced in tetramerous and pentamerous seeds with the thickest walls, best-developed bundles, and clearest dissepiments. The absence of the lagenostome in the dimerous and trimerous seeds is, moreover, conceivable as in some way connected with the great development of the stone in these latter. Taking the evidence *in toto*, therefore, it may be asserted without fear of contradiction that there is not a scintilla of direct evidence going to show the derivation of seeds with a protruding lagenostome from thin-walled forms without development of a lagenostome region. As in so many paleontologic problems, a dual interpretation is possible and here it is that the ways diverge. If the synangial hypothesis has in it elements of truth, the thin-walled seeds without noticeable development of a lagenostome are primitive, and the thick-walled seeds are the end-result of a direct and continuously progressive evolution of new structures. On the contrary, if the disk hypothesis is essentially correct, the reverse is true and the modes of testal and floral evolution are vastly more varied than hitherto conceived possible. Not only so, but both seed and floral structures have a vegetative basis and are largely the resultant of comparatively simple processes of reduction. The huge *Pachytesta* types reaching 10 cm. in length may be here recalled (1881).

With respect to the nature of the lagenostome, however, the question of reduction versus direct evolution need be left in no confusion due to mere use of terms. Oliver and Salisbury (1911) have introduced an elaborate and very usable terminology for the complex seeds of ancient time. But this should in itself mislead no one into reading into old seed apices an undue complexity of origin. For Oliver and Salisbury themselves, in their contribution on the affinities of the Paleozoic seeds of the *Conostoma* group just cited, explicitly describe a continuity of tissues in the lagenostome region. As they put the facts, "the epidermal layer of the interior of the seed is in complete continuity throughout and the various regions termed the micropylar tube, micropylar funnel, plinth jacket, plinth, and lagenostome walls are merely different and specialized portions of one and the same layer."

Taking all the facts together, therefore, the main elements in the case for the disk hypothesis of testal origin have now been stated, and it has become clear that there is no impassable hiatus between the hypothetic sterilized campanulate disk suggested by the fertile eared disk of *Cycadeoidea* and the eared disk which incloses the nucellus in the ancient seeds; while it might even be asserted that the hypothesis of sterilization and megaspore protection by greatly reduced fronds rests actually under less burden of demonstration than does the synangial theory which calls into requisition the continual evolution of new structures.

Nor is there any dearth of material of fundamental importance to the study of these greater phases in plant history. Among more recent contributions on the Paleozoic Cycadofilicaleans is a most interesting paper by Bertrand (1913). New facts are brought out concerning peculiar orbicular leaves of *Neuropteris*, which bear marginally pendent sporangia in a manner quite different from *Crossotheca*, and supposedly pertain to a handsome series of associated leafy seeds; but a careful comparison of such "seeds" with the microspore-bearing disk *Codonotheca* remains to be given. In fact, the need to reconcile this latter form with the various *Neuropteris* seeds of similar exterior has been for some time evident, and it is most interesting to recall that in Sellard's original paper of 1903 a Neuropterid affinity was pointedly suggested. Taken in conjunction with the new types of Neuropterid fructification brought to light by Bertrand, *Codonotheca*, to say the least, shows the fruits of the Paleozoic "quasi-ferns" to have exhibited an extraordinary range of structure and it is easily possible that some of the fossils considered to be Neuropterid seeds are in reality bisporangiate buds. Indeed, as more or less directly suggested on previous pages, there could scarcely be indicated a more fascinating subject of study than the internal structure of the little understood Neuropterid seeds of large leafy form, although these remarks do not apply so directly to small and winged seeds like those of *Pecopteris Pluckeneti*.

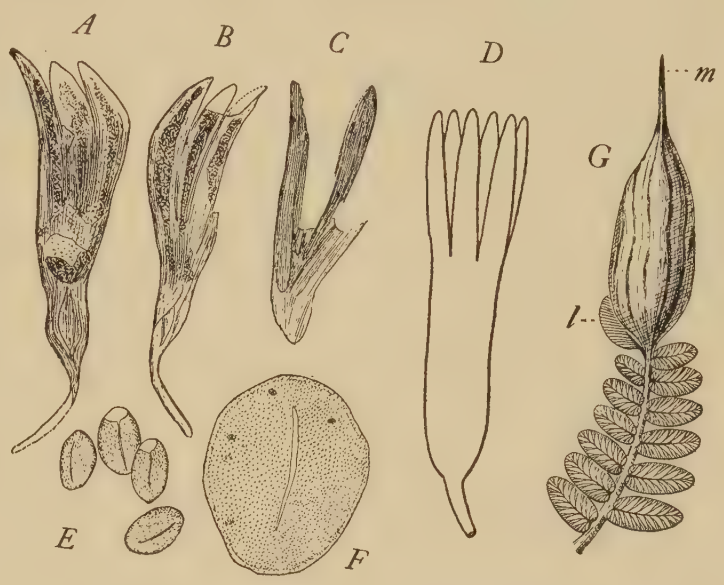


FIG. 61.—Reconstitution of Neuropterid fructification. All figures about natural size except the spores E, F, which are enlarged 28 and 85 times respectively. A–F, from Sellards; G, from Bertrand.

A–F. *Codonotheca caduca*, a campanulate microspore-bearing fruit closely associated with and probably pertaining to the *Neuropteris decipiens* foliage of the Pennsylvanian of Mazon Creek, Illinois. The interior faces of the lobes are quite covered with spores which are freely brought to view when the nodules in which the fruits occur are split open. E, F, the enlarged spores. D, restoration of the hexamerous disk. G, *Neuropteris heterophylla* with *Trigonocarpus*-like seed. *m*, the so-called micropylar beak; *l*, "demi-cupule."

IS THERE AN ANALOGY BETWEEN SEED AND FLOWER?

Is it not, then, fully significant that, as we go back into the remoter Paleozoic, seed structures are leafy and have highly developed vascular bundles, while pollen is likewise of relatively enormous size? Does not such fossil evidence as is afforded by the seed-like exterior of *Codonotheca* with the large size of its (?) microspores go to show that with continued sterilization of a megaspore-bearing crown of whorled, equitant, opposite, or cir-

cularly emplaced sporophylls finally reduced to bract-like form, these might unite to inclose a single spore, the nucellus, and thus *surround and fuse with it* as a *ribbed, bundle-supplied, apically chambered*, protecting wall? This indeed is the analogy which must best explain the seed and show why ancient seeds are the more complex, are leafy, and have their major and secondary ribs, their canopy, and lagenostome. The seed is, in short, as much a branch, or better, a compacted and sterilized crown of sporophylls, as a simply staminate flower; while a seed and its stamens is thus primarily analogous to a bisporangiate strobiloid crown, and either by itself to a simple monosporangiate crown. Just as the strobilus and the flower are the homologues of primitive crowns of simple, spore-bearing leaves, so it seems that the seed is the first resultant of a process of reduction from an apical group of fertile fronds—a dyad in case of platyspermic forms; a triad, tetrad, or pentad of such fronds in the case of more complex seeds like those of the *Conostoma* group.

Furthermore, reproduction being so completely dependent on nutritive processes primarily and on the use of protective coverings secondarily, it is certain that as megaspores increased in size, the simplest mode of protection would be inside a whorl of reduced leaves at the center of a more or less scaly bud or crown; and alike in the Devonian as in the Mesozoic the development of apical domes would best overcome the spatial requirements due to circinate or conduplicate prefloration. At least this is the explanation that comes first to hand, it being clear enough that such an outer covering would at once enable the plant to greatly increase the size of its megaspores, protect them in an economical manner from insects, rain, and wind, and then, following the assumption of microphylly with later cycles of branching and budding, greatly increase the number of fruits. So it is conceived the seed habit was acquired by a process of reduction and sterilization with final inclosure of a giant apical spore, following the forward course of evolution which first enabled plants to invade and cover the land and then raise their stems above the soil.

It does seem, then, that there is a certain analogy between a staminate flower and a seed of the older gymnospermous type, that indeed both have a common history as derivatives of homosporous crowns. But necessarily the conception of the course of change which had carried these reproductive structures far apart even in Devonian time, and the yet hidden rôle of the older heterosporous crowns, can only be cleared by the discovery of fossil evidence. So vast and multitudinous must be the course of change involved that it appears nearly impossible to hypothesize given stages in floral and seed evolution, though certain factors of change do come into view. Primarily, it seems that up to a certain point the process was one of nearly universal forward evolution, after that one of reduction, or of sterilization, whichever one chooses to call it, coupled with branching or budding—nature taking the course of least resistance rather than accomplishing the end directly by the continual evolution of new structures. According to this new view the actual amount of structural evolution is far less than once seemed could possibly have sufficed.

It would also seem clear that the first great crest in the successive waves or pulsations in the evolution of plant, and especially of floral, structures, was marked by a primitive forest—the first in which plants clothed the land and by megaphyllous and then simple stem growth raised their structures above the moist soil into the air and sunlight. And it is there, in that oldest forest, that after the direct evolution of stem, vascular, and leaf structures, the primitive strobilar crown was organized and a point established where branching and sterilization could set in and thus inaugurate that vast course of aerial flower and seed growth evolution which has gone on unceasingly since early Devonic time.

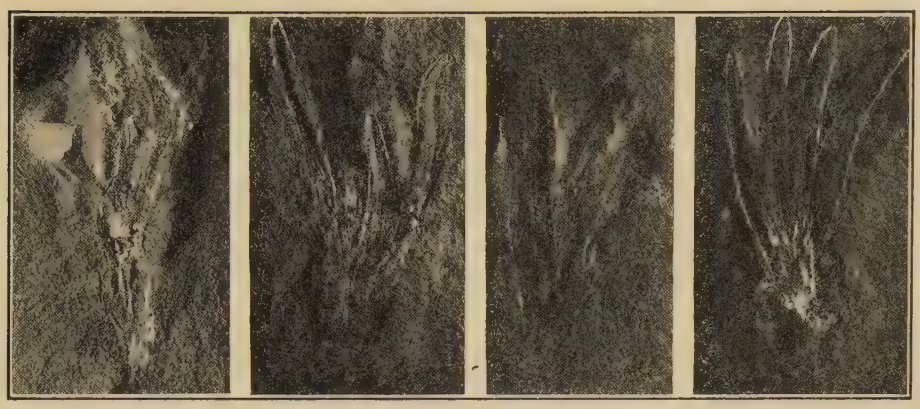


FIG. 62.—*Codonotheca caduca.*

This remarkable microsporous campanula of hexamerous type occurs in considerable abundance in the ironstone or clayey nodules of Mazon Creek, Illinois, in closest association with a varied Neuropterid foliage. These photographs of the fruits just as exposed to view by splitting open the nodules are by Sellards. They are natural size. The inner faces of the lobes of the fruit to the left are literally covered with the very large and remarkably conserved microspores illustrated in the preceding figure. The resemblance of such disks to seeds invites critical restudy of many ancient fruit imprints by modern chemical methods.

The line of argument which has just been followed in attempting to show a certain analogy between buds or crowns, seed coats, and floral envelopes will have failed utterly if it has not been shown that the conceivable modes of angiosperm origin may be greatly broadened. The definite suggestions reached are that seed and later floral evolution were not sporadic phenomena, but the resultants of an orderly sequence of change all along a front as broad as plant life itself; that sterilization and megaspore protection by fused whorls of leaves is an alternative hypothesis for early testal origin; that cupules could as readily be derived from fertile as sterile organs. In fact, it even begins to appear possible that, as far back as the Paleozoic, some very simple epicycle of seed and strobilar change in an as yet undetermined but numerous tribe may have been basal to the evolution of modern floral types; although in the closing chapter the case for a more distinctly Cycadeoid than Coniferous Angiosperm ancestry will be presented.

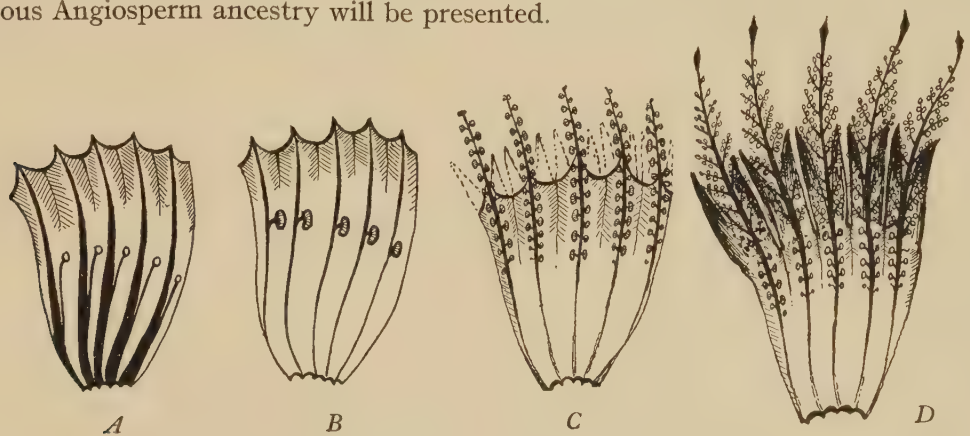


FIG. 63.—Theoretical stages in the reduction of staminate disks represented as segments.

A, any common campanulate form with simple stamens; B, hypothetical Cycadeoid disk reduced to a single synangium to the frond component; C, inner view of sector of a *Williamsonia mexicana* disk; D, sector of a *Cycadeoidea dacotensis* disk with the pair of shoulder spurs borne by each frond. (Modified from Wieland, 389.) At the time this figure was first published the pair of shoulder spurs forming the dome were unknown. The original suggestion of a certain analogy between staminate disks and dicotyledonous disks is distinctly strengthened by the ceratoid condition in *Cycadeoidea*. (See Bot. Gazette, Dec. 1909, p. 436.)

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B A

FIG. 64.—Yorkshire Coast *Williamsonia* stems with both pinnate *Otozamites*-like fronds and scale leaves attached.

A. *Williamsonia gigas* (Echantillon No. 2399*a*, Jardin des Plantes, Paris; Collection Yates, 1847). Terrain oölithique inférieure, Scarborough et Whitby. Two-fifths natural size.

B. Paris Museum specimen. Collection Yates, Yorkshire Coast Oölite, Cliffs of Hawkser and Runswick. One-half natural size.

Both slabs are sketched by Saporta in the Plantes Jurassiques. A is shown on Plate 81, figures 1, 1*a*, Vol. II, and B on Plate 242, fig. 1, Vol. IV.

CHAPTER XII.

THE CYCADEOID ALLIANCE.

The study of the silicified cycads can no longer be kept wholly separate from that of the casts and imprints which constitute the main part of the Cycadophytan record. From Permian time to the close of the Cretaceous, Cycadophytan leaves, fruits, and stems (as is now known to be the fact) are of widespread occurrence in quite all lacustrine or fluviatile deposits of the globe. At the time of the publication of Volume I the relation of the silicified series to the imprints was only beginning to be understood; and it was found most convenient to illustrate the general characters of silicified stems by giving a more or less formal account of the existing Cycadaceæ. But so direct has been progress in the study of the Cycadophytans during the past ten years that very few of the characters of the silicified stems remain unparalleled in the imprint series. In fact, these two series so merge into each other that the data of the foregoing pages would in a large sense remain needlessly isolated and incomplete without the addition of a résumé of the main facts known about imprints and casts. Such a résumé may best be based on a preliminary account of the Williamsonian tribe published with reference to further use in this volume and on the investigations of the Liassic floras of Mexico (391, 394, 396); especially, also, on the long and important series of contributions by Nathorst (186, 187, 189, 191, 193, 194, 195, 197, 198, 199, etc.), together with valuable papers by Seward (284–288), Krasser (133, 134), Thomas (329, 331), Thomas and Miss Bancroft (332), and Miss Bancroft (13).

The present object is, then, to show in a simple manner the general alignment of the Cycadophytes and especially to describe, from a biologic viewpoint, the features of the long problematic Williamsonians taken as the type of a great and dominant Mesozoic group to which the silicified cycads afford the indispensable structural key. Obviously, in so dealing with a cosmopolitan alliance with constantly enlarging but undefined borders, it is more convenient to speak of groups or tribes than of families or orders; also the silicified Cycads or Cycadeoideæ of Robert Brown, 1828, are arbitrarily separated from the Williamsoniæ, Carruthers, 1870, although the line of demarkation between these families is vague. In singling out the genus *Williamsonia* as a tribal or group type it is intended to likewise accentuate the order of discovery, although it is important to point out that this genus is by no means the most interesting of its tribe thus far restored. That distinction unquestionably belongs to *Wielandiella* of the Rhät of Skone, so ably and skillfully studied by Professor Nathorst by means of chemical methods (194).

It is but a few years since it was held with little question that the common types of Mesozoic cycadophytean leaves must all pertain to plants belonging to true cone and carpellary leaf-bearing Cycads near to existing types, or at least to ancestral forms of strictly Cycadalean aspect. True enough, Williamson (402), from long study of the specimens collected by himself and his father along the Hawkser and Runswick cliffs of the Yorkshire coast early in the last century, had reached, about 1870, an excellent restoration of his "riddle" *Zamia gigas*—renamed *Williamsonia gigas* by Carruthers (65). But, as Carruthers had meanwhile found, the Isle of Wight silicified trunk *Bennettites Gibsonianus*

had an ovulate fructification so different from other gymnosperms that its characters suggested no relationship to the imperfectly known *Williamsonia*. Precisely because of this unique type of ovulate cone it was not seriously suspected that the great majority of fossil cycad trunks bore fruits like it or could be other than ordinary cone-bearing forms; and the foliage being unknown, the claim of variety of structure and relationship in Cycadophytan imprints rested solely on the evidence brought forward by Williamson in his reconstitution of *Zamia gigas*. The correctness of this was disputed. Briefly the case stood

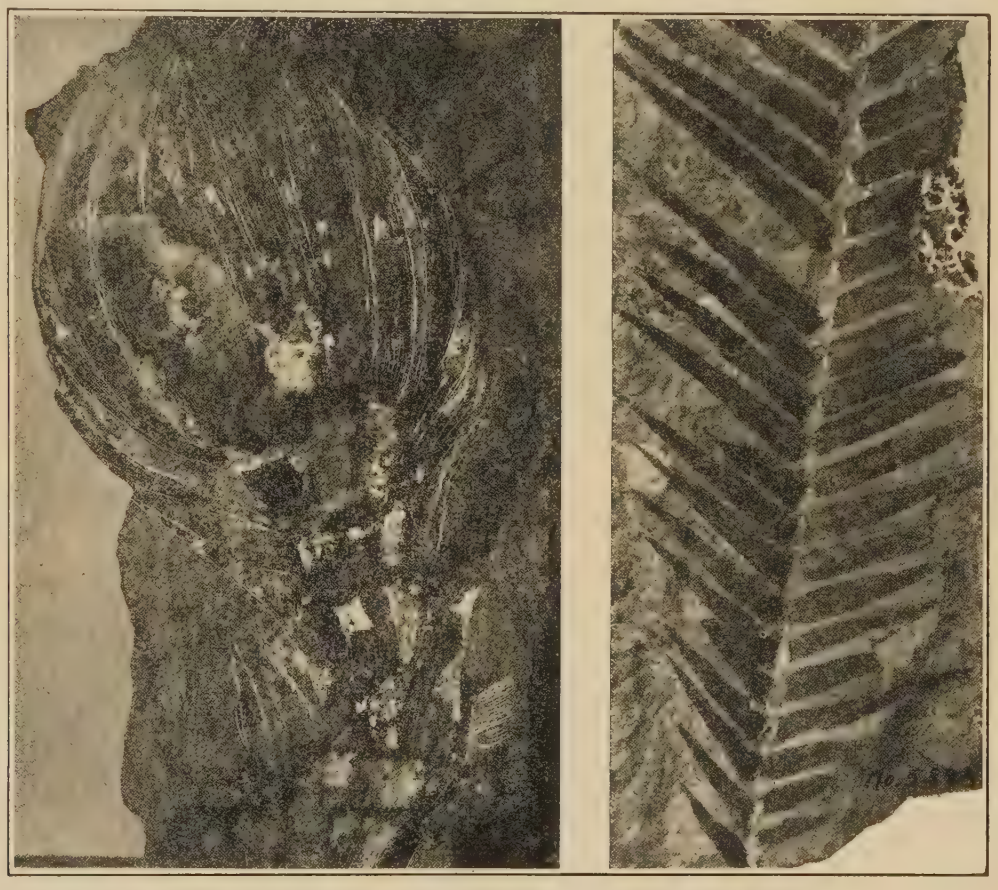


FIG. 65.—*Williamsonia gigas*. Fruit bud attached to bract-enveloped peduncle, and an accompanying frond from the Hawkser and Runswick Cliffs of the Yorkshire coast.

The bud is a Paris Museum specimen of the James Yates collection, so rich in both fruits and fronds of several species. The slightly retouched photograph is about natural size. The frond is only two-fifths natural size and of a different species or variety from the frond-bearing stem of figure 64.

thus. Saporta (242) with the splendid James Yates collection of Williamsonias brought to the Paris Museum by Brongniart in 1843—a collection including the fine stem with leaves attached illustrated by figure 64, and equal if not superior to any that remained on English soil—rejected the idea of any organic connection between the Williamsonian "pyriform axes" and "carpellary disks" and the "*Zamia gigas*" fronds. In this he was followed by most continental botanists, with various suggestions as to the possible affinities of the Yorkshire coast specimens, ranging from the Cordaites-like *Yuccites* (Schimper, 250) to *Orobanche* (Nathorst, 186).

Thus the idea that complexity of structure might lie hidden behind the great array of Mesozoic Cycad stems and leaves failed of development and study and received but scant mention in paleontologic texts; and so the subject rested until the structure of the *Cycadeoidea* flowers was at last elaborated from the American specimens, and the true position of *Williamsonia* as the representative of a slender-stemmed family closely related to the Cycadeoideæ was made apparent. Collateral evidence has now so accumulated that nothing in paleobotany is more clearly established than that a great complex of Williamsonia-like plants, including other families yet to be determined, spread over the earth in

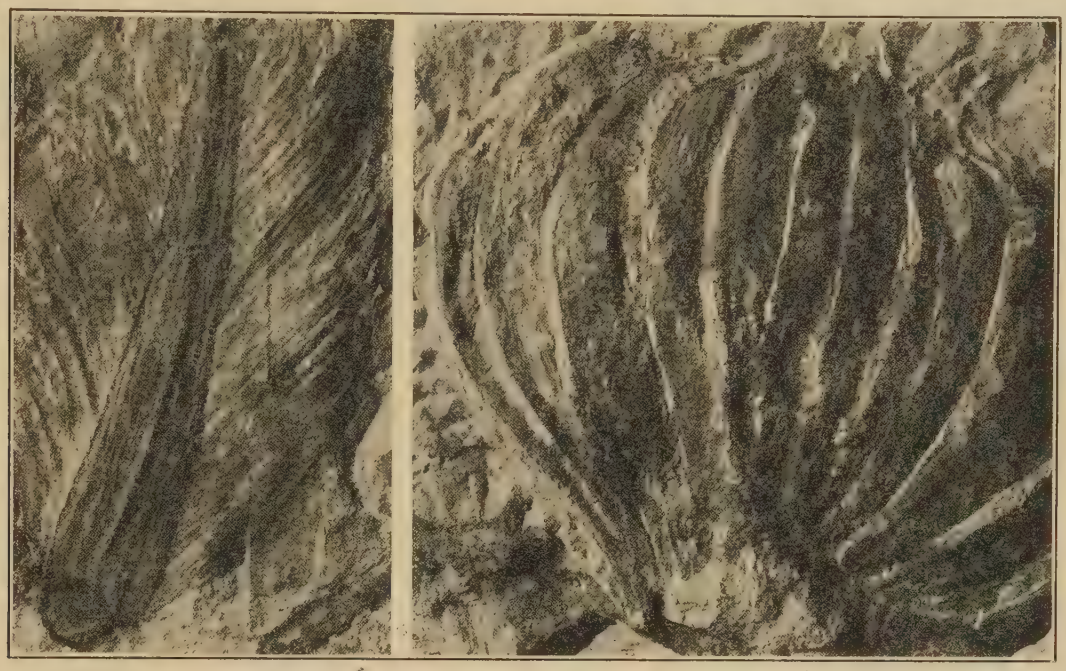


FIG. 66.—*Cycadolepis mexicana* and *Williamsonia xicotencatl* as found closely associated with stems and large fronds in one of the quarries opened by the writer on the Rio Consuelo of Oaxaca, Mexico. Both ramentum-covered scale and flower-bud are natural size.

These specimens probably belong to one and the same plant with stems like those of figure 73 and leaves like those of figure 67, all being found in the same slabs. Only in the case of the leaves is there some doubt because of their size. As several species of both foliage and fruits occur together, it would be necessary to find actual contact of leaf, fruit, stem, and scale before attempting restorations.

the Mesozoic. As Scott has said, the application of comparative criteria may lead one to the conclusion that 30,000 to 40,000 of these species existed in Mesozoic times. Moreover, every year that goes by strengthens the view that of all post-Paleozoic gymnosperms the type represented by *Williamsonia* is the one most generalized, plastic, and capable of floral variation; for the silicified trunks of the near family Cycadeoideæ are simply the specialized relatives, capable of fossilization as entire plants with their flowers conserved in that exquisite perfection which has so advanced our knowledge of Cycad structure and growth. They are the structural key to their race, without which it would not have been possible to decipher even by the more refined methods of fossil imprint and cast study developed in the past few years, either the true floral structure of *Williamsonia* or the full extent of its cycadofilicalean relationship. But this great service once rendered, the silicified series wholly fails of the extended interest of the allied casts and imprints, among which lies our great hope of future discovery not only of critical anatomic features, but eventually of the ecology and larger history of the Cycadophyta. In short, the narrow

structural range of the silicified trunks, well-nigh expressible in the terms of a single genus, is only what might be hypothesized from the features of a single species like *Cycadeoidea dacotensis*, were it the only known form. These are then the stereotyped terminal forms of a side branch from a great plastic and dominant precursor race, unquestionably including the vast bulk of Cycadophytan vegetation from the earliest Triassic to mid-Cretaceous times. We thus see in the Williamsoniæ the representatives of a vast Mesozoic plexus derived from a Paleozoic quasifern ancestry in which pro-angiospermous characters, whether ancestral to angiospermous features or not, are ever surely and obviously engrafting themselves; and we conceive this plexus to contain many discoverable forms of great variety in size, foliage, branching, and floral types, displaying every phase of monœcism, diœcism, and bisexuality, coupled with a continuous series of sporophyll reductions, sterilizations, and increasing flower output.

FIG. 67.—*Otozamites* (*Williamsonia*) *oaxacensis*. ×1. One of several species of fronds found most closely associated with the scale leaf and fruit-bud of figure 66 in the Liassic strata of the Rio Consuelo, Oaxaca, Mexico.

CYCADOPHYTAN FOLIAGE OF THE MESOZOIC.

Considering the fact that the fresh-water deposits of the Trias and Jura are of far more limited extent than those of later age, the amount of Mesozoic Cycadophytan leaf material is large. But it is not the purpose to enter into any detailed description of the several Williamsonian genera, nor is it necessary to describe the more important sections from the localities yielding Williamsonian material. It may suffice to illustrate a few of the more characteristic early Liassic forms recently collected by the writer from the Rio Consuelo section of Oaxaca, Mexico, and compare these with material previously known.

Referring to figure 64, the Yorkshire coast stem there illustrated was long the only known Mesozoic Cycad with foliage attached. Two leaf-bearing nodes are separated by a scale-leaf-bearing internode about 8 cm. in length. The stem continues above as a forked and bract or scale-leaf-covered prolongation. One of these younger branches may have been fertile, the other vegetative, as in some pines. The fruits of Cycadeoid type may have been bisporangiate or not. The plant may have branched freely, as *Cycas* rarely does, and was of composite type, forming a connecting link between the Cycads and Cycadeoids.

The scale-leaf-enveloped stem fragment of figure 64 certainly has a *Cordaites*- or even a *Yucca*-like aspect if taken by itself, and it will be recalled that Saporta connected these stems with the *Williamsonia* fruits, which he did not regard as borne on the associated plants with Cycad-like leaves. Evidently the stem segment illustrated may be of a different species from the *Williamsonia gigas*. In any case scale leaves must have varied greatly in development, and the length of the scale-leaf internodes would vary in even the same plant from year to year. Curiously enough, no stem has ever been found with *Cycadolepis* scales attached, although it is possible that those of the type shown in Figure 66 pertained to the stems of Figure 73 A, B, with which they were found associated.

The Oaxacan frond of Figure 67 is from the same quarry as the specimens of Figure 66; but still more closely associated ovulate cones (Fig. 79), as well as other frond species, prevent a positive restoration of any one species. Thomas (329) figures as *Otozamites giganteus* a closely related frond segment from the Jurassic of Kamenka in which the somewhat longer and slenderer pinnules reach a length of over 10 cm. The maximum pinnule size in the Williamsonians is, however, attained by several species associated with the frond of the present figure 67. In one of these, named *Otozamites Diazii*, the pinnules are 15 to 17 cm. long and 3 cm. broad. An accompanying isolated pinnule 5 cm. broad, evidently of a yet different and still undescribed species, was also found. These dimensions are far exceeded by some of the existing Brazilian and other cycads. The microphyllous frond types of Figures 69–71 are far more representative of the size reached by the Williamsonians. The *Noeggerathiopsis* of Figure 68 is included for the double purpose of illustrating the similarity to some of the *Podozamites* pinnule types as well as Cycadeoid scale leaves, and also accentuating the fact that *Cordaites* was closely associated with typical Williamsonians in the lower portions of the El Consuelo section. Fronds closely allied to *Otozamites Molinianus* and conserved in great perfection with partial carbonization occur on the same slabs which bear the leaves of *Noeggerathiopsis*.

The *Anomozamites* of Figure 68 is also from the lower portion or *Cordaites* zone of the El Consuelo section, but is scarcely distinguishable from the Indian forms figured by Feistmantel. The precise relation of this plant to *Wielandiella* (Vol. I, Fig. 12) remains for

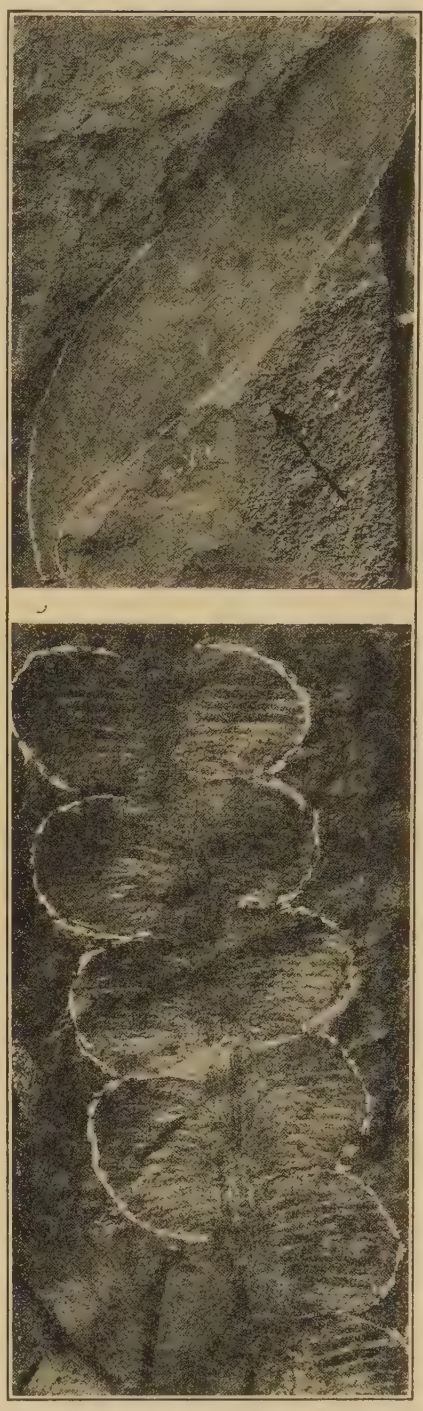


Fig. 68.

Fig. 68.—*Noeggerathiopsis* sp. (Cf. *N. Hislopi*) above. Below, a frond fragment of *Anomozamites* sp. (×3). (Cf. *A. Lindleyanus*.) These are typical older elements of the lower plant beds of the Rio Consuelo of Oaxaca. See pages 199, 200 for remarks on the age of these early Liassic plants.

the future to disclose. It is probable that a great variety of primitive Cycadophytans had this general type of foliage, which suggests resemblances to the foliage of seed ferns on the one hand and the Pterophyllums on the other.

Figure 69 (above) illustrates an *Otozamites* type which may ultimately prove quite different from apparently similar mid-Jurassic forms, and suggests a transition in the direction of the Permian *Plagiozamites* with oblique crescentic pinnule insertion. It is, however, closely associated with the *Otozamites hespera* (Fig. 69, below), a frond type which passes well up into the Jurassic and is distinctly cosmopolitan. It is important to observe that the obovate or spatulate frond form here exemplified is very characteristic of the Mesozoic. It occurs in various species both larger and smaller than the present. Some of the Pterophyllums also have this form, notably the small *Pterophyllum fissum* of Feistmantel from the Indian Jurassic, in outline recalling some small irregularly segmented dicotyl leaf. If such leaves were ever characterized by the slightly netted venation of *Gnetum* or *Welwitschia*, they would represent the hypothetic transition from *Pterophyllum* to pinnatiform dicotyl leaves.

Ptilophyllum acutifolium is an abundant form in India, on the Yorkshire coast, and especially in Mexico, characterized by the form of pinnule insertion on the rachis, the anterior edge being free and rounded, with the posterior basal edge decurrent. The form is therefore intermediate between *Pterophyllum* without free bases and the double-eared *Otozamites*. In the middle portions of the El Consuelo section the Ptilophyllums are found covering large slabs in the greatest profusion. They vary much in size in both Mexico and India. In Figure 70 (above) a young crown of fronds is illustrated in the natural size. These fronds belong to one of the smaller varieties and the stem bearing them could not be large. Evidently further search must reveal the stems with the leaves attached.

The frond of Figure 70 (below) can scarcely be placed in the genus *Pterophyllum*. It rather represents the intermediate form between *Ptilo-*

FIG. 69.—*Otozamites tribulosus* Wieland (above) with *Otozamites hespera* Wieland (below). Both natural size. Two characteristic and closely associated frond types from middle part of lower plant beds of Rio Consuelo, Oaxaca, Mexico.

phyllum and *Otozamites*, although retaining resemblances to *Pterophyllum*. This frond type is widely distributed in the mid-zone of the El Consuelo section and has been found elsewhere in the Oaxacan region. It is one of the most characteristic of the microphyllous Williamsonian types.

The singularly handsome frond species *Otozamites lucerensis* (Fig. 71) varies but little from the foregoing form. On the original specimen the pinnule outlines and venation are throughout distinct. This frond type is also intermediate to some of the forms longer known. On the one hand the oblique close set of the pinnules on the slender rachis suggests the *Plagiozamites* type of insertion, while on the other the short, broad pinnule is but little removed from the more orbicular pinnules of the likewise narrow and elongate frond *Otozamites Mandelslohi*, common alike to the Lias of Franconia and Oaxaca.

The foregoing are only a few of the many types of Williamsonians which could be illustrated with profit; but they serve to show something of the great variety of leaf types, the variations in form falling well within the limits of a homogeneous group. It is not until one passes back into the Permian that the Williamsonian leaf type is found little in evidence or merges into more distinctly primitive forms not readily separable from the foliage of seed ferns. A working definition of the various Williamsonian frond genera may be found in a recent contribution by Halle (107).

DOMINANCE OF CYCADEOID FOLIAGE TYPES.

The Williamsonian foliage being in all but the rarest cases isolated from stems and fruits, the primary value of the species is stratigraphic. To the future belongs the labor of homologizing, so far as may eventually prove possible, the isolated *Cycadophytan* foliage and fruits, usually found associated with not only other fragmentary and distantly related plants, but with conifers, the last of the seed ferns, persistent Cordaitaleans, and other little-known relatives of these gymnospermous types. As every collector knows, the utmost circumspection barely suffices in drawing inferences from association of isolated organs of fossil plants. Behind a thickness of a few centimeters in a sedimentary plant-bearing rock, or a mere joint or separation plane, may lie the hidden change of a river bed, the cutting away of a bank in a different plant community, or perchance a year of time with its change of winds and uprooting storms. Indeed, with such factors added to the infrequency of stems, absolute proof

FIG. 70.—*Ptilophyllum acutifolium* var. Crown of young fronds (above). Full-grown *Otozamites Reglei* var. (below). Both figures natural size. Respectively from middle and upper plant beds of Rio Consuelo, Oaxaca. See text.

of leaf, stem, and fruit unity is generally so difficult to establish that the claim for a great extent of the Cycadeoid alliance rests chiefly upon the recurrence of the isolated species in widely separated localities.

Yet the recent field work, especially on the Yorkshire coast (194, 197) and in the newly discovered Mixteca Alta localities (396), has minimized the uncertainities more than might have been anticipated, and will still further do so. The argument for a heavily preponderant Williamsonian element in the Cycadophytan foliage of the Mesozoic, with a lesser Cycadeoidean series and a nearly negligible Cycadacean representation, is, then, chiefly one of analogy and association. The evidence may thus be summarized:

(1) The only known Mesozoic Cycad stems with leaves or fruits attached are Cycadeoidean and Williamsonian (*cf.* Vol. I, Fig. 12, and Fig. 64); and now that it is seen that the nodes of lesser scars in forms like *Wielandiella*, as well as *Yatesia* and *Bucklandia* (Fig. 74), do not necessarily indicate a succession of scales and carpellary leaves, scarcely a single Mesozoic Cycad stem is left free from the suspicion of belonging to the Williamsoniæ. Just as all the silicified trunks have finally proved to belong to the Cycadeoideæ, so now either that family or the Williamsonian tribe threatens to absorb the entire series of stem imprints and casts. The proof given in the description of *Cycadeoidea Dartoni* that some of the leaves of the silicified series have the doubly eared or *Otozamites* form gives further support to this statement. In fact, Mesozoic stems indisputably belonging to the Cycadaceæ are most difficult to cite, it being the generalized and far more varied Williamsonian types along with the earlier Medullosan forms that make up the known record.

(2) The recurrence and association of strobili and fronds is strikingly the same on the Yorkshire coast, in India, and in Mexico; and while in each of these great Williamsonian fruit-yielding regions the fossil plant series is a most varied one, carpellary leaves and cones of Cycadaceæ are exceedingly rare or absent. Nor are they ever abundant in the other frond-yielding localities of the globe (*cf.* Figs. 87–89), in most of which Williamsonian fruits probably occur. The wealth of these latter fruits, on the contrary, is fully attested by the discoveries of the past ten years. Thus Nathorst and Halle on the Yorkshire coast, and the writer in the Mixteca Alta, have added perhaps a dozen species to the *Williamsonia* ovulate cone series, and shown the immense fossil wealth of the new quarries located in both regions, though true Cycadaceæ remain quite as scarce as before. Indeed, it lends no little emphasis to this fact to observe that, among all the *Williamsonia* collections made in Oaxaca, there occurs just one single group of carpellary leaves, poorly conserved, but with the medium-sized seeds plainly indicating a species of *Cycas*, while no cycadacean cones whatever were recovered.

FIG. 71.—*Otozamites lucerensis* sp. nov. ×1. Near *O. Reglei* Brong. A typical microphyllous frond with slender rachis from the upper plant beds of the Rio Consuelo of Oaxaca.

(3) Collateral evidence that the Mesozoic leaf genera form two homogeneous series of Cycadophytans differing broadly from the existing Cycadaceæ is also afforded by a study of the cuticles recently carried out by Thomas and (Miss) Bancroft (332). Evidently the stomata and epidermal cells indicate to some extent the larger gymnospermous relationships. In the Cycadophytan alliance some characters have undergone little modification since Jurassic time and are therefore scarcely to be regarded as due to local or temporary conditions of environment. Considerable similarity in stomatal structure exists in the group of genera including *Ptilophyllum*, *Zamites*, *Otozamites*, *Anomozamites*, and *Dictyozamites*, all of which are doubtless typical Williamsonian genera. A second group includes *Ptilozamites*, *Nilssonia*, and *Ctenis*, which it is even suggested might be separated as the Nilssoniales. In the first group, which is of most importance in the present connection, the stomata occur only on the lower side of the leaf and are usually absent below the vein courses; the usual position is at right angles to the veins. For the numerous details of stomatal structure worked out by Thomas and Bancroft, their original paper must be consulted, and it will be found of considerable interest to at the same time refer back to the descriptions and figures of fossil stomata given by Bornemann in 1856. The stomata of *Cycadeoidea ingens* figured by the writer (397) broadly resemble those of the Williamsonians in form and position, but being found on the young unexpanded pinnules are, as might be expected, a trifle simpler in outline.

(4) The histologic features of the *Ptilophyllum* pinnules strongly confirm the inferences drawn from the development of stomatal features in this and other frond genera of the Mesozoic. For reasons given under the head of stem structure, the silicified trunks from India with *Ptilophyllum cutchense* leaves attached of the type first figured by Oldham and Morris in 1863, later Seward (279, Fig. 30), must be regarded as typically Williamsonian. These interesting fossils have recently been studied by (Miss) Bancroft with no little success, considering the porcellanous nature of the material. As in *Cycadella*, the transversely cut rachidal bundles outline a heavy V. The pinnules also prove to have essentially the same development of hypodermal sclerenchyma, conspicuous bundle sheaths, and other features seen in the pinnules of *Cycadella ramentosa*. As in that form, there is an absence of the strong junction of the hypodermal sclerenchyma and bundle sheath seen in *Cycadeoidea ingens*, and in the leaves illustrated on Plate 57. This junction is probably characteristic of the foliage of most large-stemmed Cycadeoids; but that such would have the more strongly marked xerophyllous features is in any case the reasonable inference.

All the figures which have ever been published showing Cycadeoid pinnule structure are those given in the preliminary study of 1899 (373); in 1905 in U. S. Geol. Sur. Monograph XLVIII, Plates LXII, LXIII; in Volume I; and lastly those of Bancroft just cited. But the evidence of pinnule structure in the Williamsonian type may be regarded as conclusive, and in full accord with that afforded by the study of other vegetative and the reproductive structures of both the imprint and silicified series.

Such, then, are the valid reasons for seeing in Mesozoic cycad vegetation a preponderance of Williamsonian types making up a great tribe or alliance beside which the few and little-known Cycadaceans are inconspicuous. But precisely because of this varied alignment and the certainty that relationships to the Coniferales and Ginkgoales must be more pronounced than later on, it is most necessary to avoid going beyond the inferences that can only apply to the various floras taken in bulk. With the exception of the greatly varied and cosmopolitan *Otozamites*, none of the frond genera can be arbitrarily called Williamsonian. Whatever the presumptive relationship, the given genera are always of uncertain position.

Thus the Greenland *Cycas Steenstrupi*, long familiarly cited as a true boreal *Cycas*, has been found by Nathorst to represent a hitherto unsuspected genus *Pseudocycas* of uncertain family (191); while *Zamia*-like leaves have been found closely associated with carpophylls in the Lettenkohle of Apolda (67).

Generally speaking, it is in the case of *Podozamites* that most uncertainty exists, partly because the pinnule character resembles more nearly that of Zamiaceans, partly because of the probability that some of the included forms are broadly related to the Coniferales. Nathorst (196) has discovered that *Cycadocarpidium* is a loosely compacted strobilus of very leafy two-seeded megasporophylls, so intimately associated with and so like the leaves of *Podozamites* as to leave little doubt that the principal Jurassic-Rhätic fossils referred to these genera are leaf and fruit of the same plant.

On the basis of the strobilus alone, a primitive leafy cycadaceous type (such as is readily pictured from abnormal cones of *Encephalartos* described by Thiselton-Dyer, or those of *Zamia* brought to notice by Wieland) would at once be inferred. But it is also shown by Nathorst that the leaf-laminæ of *Podozamites* are not all laterally borne pinnules of a once-pinnate frond as hitherto considered, but are in part the spirally borne leaves of small scale-covered stems of presumably limited growth and distinctly coniferous habit; from which it is obvious enough that *Podozamites* is in part perhaps the first form ever determined from that unknown borderland between cycads and conifers.

Thus the reference of *Podozamites* to the Williamsonian alliance is brought under suspicion; though it must be remembered that the presence of the small branches accompanying *Cycadocarpidium* (or better *Podostrobus*) does not take away from the possibility that the as yet wholly unknown microsporophylls were of more or less distinctly leafy to Williamsonian type.

If we call to mind, however, the comparative paucity of Cycads of any kind in the Tertiary, and the certainty that very few *Williamsonias* passed beyond the Cretaceous, it does seem a fair inference that these latter not only made up the great bulk of Mesozoic cycadophytean vegetation, but that contrary to all previous views, true Cycadaceæ have never been markedly more abundant in species at any time in the past than they are to-day.

OCCURRENCE OF FROND GENERA IN TIME.

Omitting aberrant and little-known forms like the bipinnate *Ctenis* and the older *Cordaites*-like forms, as well as *Noeggerathia* and *Plagiozanites*, there are about a dozen more or less indefinitely separable genera of representative Cycadophytean leaves with either direct or analogic evidence of Williamsonian affinity. Their general foliar relations, culmination, and extinction are simply set forth on the opposite page.

So far as fossil preservation goes, *Pterophyllum* and *Zamites* are the representative ancient lines, with *Sphenozamites* as a relative merely characterized by oddity of leaf form. And these old lines pass on to add their quota to the great Williamsonian group of the Rhætic, the period of most rapid evolution. Culmination occurs in the lower Jura, while extinction begins in the middle Jura and progresses steadily to the upper Cretaceous, where the Cycadeoideas also find their final representation in both Europe and America.

Were tabulation extended to the one hundred or more species referred to the Mesozoic frond genera, the origin and extinction curve might likely remain quite the same as when the genera alone are considered, though any such fuller elaboration of the data of species must remain in abeyance until considerable comparative work with better collected and prepared specimens in hand has given generic, to say nothing of specific, determination the needed accuracy. For instance, the genus *Glossozamites* is by no means so isolated as might usually

be inferred. The superb fronds from the copper mines near Abiquiu, Rio Arriba County, New Mexico, called by Newberry (205) *Otozamites Macombii*, are very near to *Glossozamites Zitteli* Schenk, being indeed a transitional form between the latter species and *Otozamites*. Also the Permian *Plagiozamites* may prove to have Oaxacan representatives. The genus *Anomozamites* is correctly retained by Nathorst for isolated fronds like those of *Wielandiella*, the latter name being confined to the Skone form with leaf and fruit attached to the small branched stems. It appears that the Cycadophytan elements of Triassic time must be found more varied than is here indicated.

The Cycadeoid Alliance:

Pterophyllum Series (Pinnule base entire): Pterophyllum, Dioonites (?), Nilssonia (?), Wielandiella.

Zamites Series (Pinnule base contracted): Podozamites, Ptilophyllum, Zamites, Otozamites, Sphenozamites, Glossozamites, Sewardia, Dictyozamites.

Cycadeoid culmination and extinction.

	Triassic.	Rhætic.	Jurassic.			Cretaceous.		
			L.	M.	U.	L.	M.	U.
Pterophyllum	⟵						⟶	
Zamites	X							⟶
Podozamites		X					⟶	
Dioonites		X					⟶	
Anomozamites		X				⟶		
Nilssonia		X					(?)	(?)
Glossozamites						⟶		
Sewardia					X	⟶		
Otozamites		X			⟶			
Sphenozamites				⟶				
Ptilophyllum			X	⟶				
Dictyozamites			X	⟶				
Wielandiella		⟶						

In general it appears that far more emphasis can be placed on the last as compared with the first reputed occurrence of the various genera as tabulated, for the simple reason that the Tertiary superficies of fresh-water deposits is far greater than that of the Cretaceous. It is always the specialized and longevous forms which are most likely to be found.

In commenting on the recovered plant series the following views were advanced:

"The fossil plant record is, we contend, sufficiently well known to draw the main conclusions as to culmination and extinction in the case of a large and cosmopolitan group like these cycads, nor is there anything in all the paleontologic record more impressive than the manner in which, following the steady disappearance of seed fern and Medullosan types, the Williamsonian alliance quickly spread over the earth and then 'disappeared' before the invasion of the Angiosperms."

The conceptions gained from continued study, however, lead to a sharp modification of this view. Any later relation between "seed ferns," conifers, cycads, and the angiosperms is not satisfactorily established, or seems less impressive than formerly. That all these lines may have been already separate and distinct at the base of the Carboniferous is not impossible. Entirely too much has been made of the absence of recognizable angiosperms in pre-Cretaceous formations; and too little significance has been attached to the one-sided lowland character of most of the older Mesozoic and the later Carboniferous floras.

OLDER CYCADOPHYTAN LEAF TYPES.

Cycad leaves, as we know them, were fully differentiated in the Permian or earlier, and reached variety within their somewhat stereotyped limits in the Trias. But there is excellent reason for supposing that the most ancient type of Cycadophytan leaf was of more or less Marattiaceous aspect. At least Cycadofilicalean foliage has this general appearance, so far as known. Nevertheless, ultimate relationships to other gymnosperms, especially the Cordaitales, and eventually even to angiosperms, must also have found clear expression in the foliage of the later Paleozoic. It is plainly the more conservative or specialized cycad and coniferous genera that now survive; in both groups the sameness of foliage is but the expression of stability, and wholly deceptive when we try to picture the more varied foliage in earlier and plastic stages or lesser plastic groups of these gymnosperm lines. Even so, in the *Zamia* of Figure 86, a strongly dichotomous venation is seen to give rise to a sparse false netting. And the gap between such a form and the long-mesh net-veined cycad *Dictyozamites* is not so great, nor yet that between the latter and a true type of mesh netting, such as that of presumably archaic dicotyledonous forms like *Cissites* and *Vitiphyllum*, or *Liriodendropsis;* or again *Gnetum gnemon*. Nor is it unreasonable to infer a transition from a frond with few pinnules, as in the Oaxacan *Zamia* just cited, to a single blade, whether in the case of parallel or net-veined types. Also, it may prove significant that not once among the great Permian series of *Ginkgo* leaf types does a transition from dichotomous to netted venation occur, but exactly among the Cycads as characterized by yet other definitely proangiospermous features.

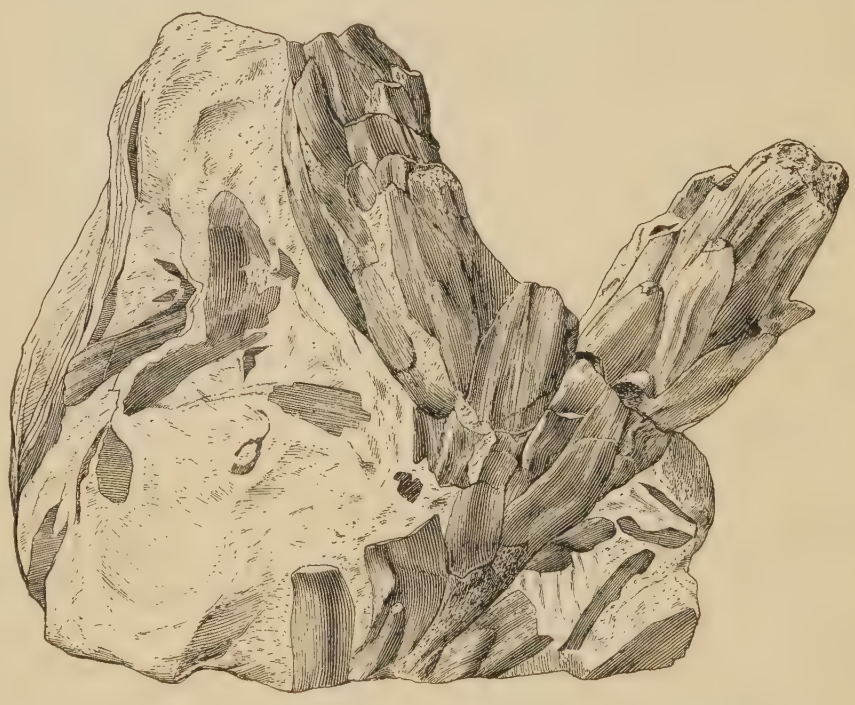


FIG. 72.—*Williamsonia* species. ×½ nearly. Bifurcate scale-leaf-covered stem, or possibly stem and peduncle, on fine-grained sand stone slab containing fragmentary cycad and other foliage. (Yorkshire coast Liassic, Cliffs of Hawkser and Runswick, 1843 or earlier. Yale—James Yates Coll.).

TRUNKS OF WILLIAMSONIÆ.

So far as critical structures go, knowledge of Williamsonian wood types has not kept pace with that of either the foliage or flowers, despite the fact that more or less imperfect casts and imprints of various kinds of stems are of constant occurrence in the cycad-yielding terranes. Williamson early noted the slender stems of cycadaceous character so persistently accompanying the *Zamia gigas* fronds and fruits of the Yorkshire coast as to justify belief in organic connection; and the restoration given in 1870 under the name *William-*

sonia gigas has come to be regarded as affording a realistic picture of the more columnar Williamsonians. A few years later Feistmantel found other yet slenderer types with short nodes of smaller scars regularly distributed along the stem. These were always associated with the fine Williamsonian buds and foliage of the Gondwanas of India, as Oldham and Morris had indeed noted at an earlier day (207). Seward in 1897 called attention to the facts clearly indicating that the Yorkshire coast stem (fig. 64) was of Williamsonian type; while Nathorst soon satisfactorily established the unity of the slender, much-branched stems, *Anomozamites*-like fronds, and fruits of Williamsonian affinity, recovered from the Rhät of Skone. First restored as a *Williamsonia* (189), this interesting plant, as is since learned from Professor Nathorst's renewed study by chemical methods (194), has a staminate form quite as much reduced as, or even comparable to, that of *Tumboa*, necessitating a new genus, *Wielandiella*.

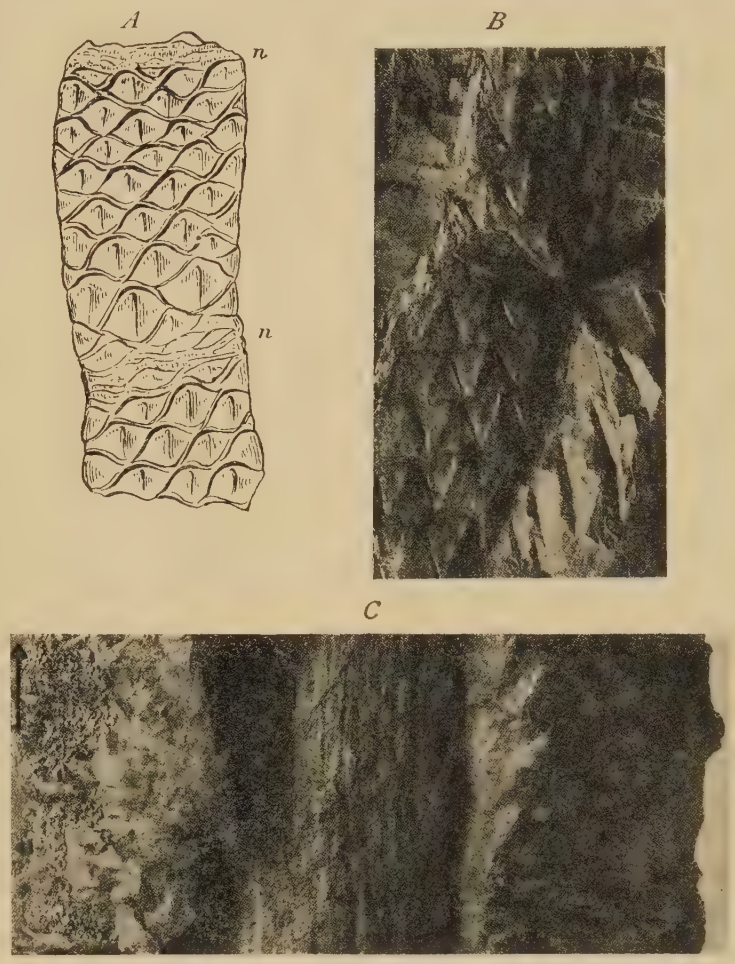


FIG. 73.—Cycadeoid stem types compared. A, B, crushed casts of *Williamsonia* stems from the Liassic of Oaxaca. ×1. C, partly "barked" stem of a Black Hills trunk (Y. 56) *Cycadeoidea Stilwelli* (?). ×½.

In many Williamsonian stems short nodes of excised foliage-leaf bases (*n*, *n*) alternate with scale-leaf bases, which are much less subject to excision; whereas in the *Cycadeoidea* stems the pith is large, the interspersed leaf and scale-leaf bases very persistent and little subject to excision. From the stem *C* a portion of the armor with the adhering cortical parenchyma and thin phloem region of the woody cylinder has split off on the cambial surface. As thus divested of its armor, or *barked*, such a stem is little larger and little different from some of the Williamsonia stems, while the resemblance to an ordinary barkless coniferous petrified stem is nearly complete.

More recently still, the validity of these determinations of leaf and stem unity, based mainly on data of association, has been confirmed by the writer's discovery of the recurrence in the Rhät-Liassic of the so-called "Mixteca Alta" of Oaxaca in southern Mexico, of precisely the same association of stems, leaves, and *Williamsonia* buds as in the Gondwanas (391, 394). In fact, the general features of the Indian specimens are so nearly repeated that Feistmantel's figures would well-nigh answer for their Oaxacan counterparts as shown in figure 73, A, B.

Similarity even extends to the stem nodes of vertically compressed scars, a most interesting feature completely establishing relationship with *Wielandiella*, in which such nodes are also present and must be due, since we know both the ovulate and staminate fructification, to scars left by leafy crowns alternating with long scale-leaf bearing internodes.

The Williamsonian nature of these stems is therefore mainly attested by their notably close and persistent association with *Williamsonia* foliage in India and Mexico, and the

presence of the nodes of closer set horizontally elongated scars, as in *Wielandiella* and the *Williamsonia gigas*. These nodes were noted by both Oldham and Morris, and by Feistmantel (88), both of whom give figures. Oldham and Morris in particular seem never to have doubted the Cycadaceous [and therefore Williamsonian!] nature of stems characterized by such nodes of larger and lesser scars, because of association with *Ptilophyllum* and *Dictyozamites* (*Dictyopteris*) foliage. In 1863 they figure for the first time silicified stems with basal parts of fronds attached and state that they examined the wood in thin sections, finding bordered pits on the radial tracheidal walls (207, p. 35, and Plate XXIV). But Feistmantel, though likewise supposing such stems to be Cycadaceous and Williamsonian, has in one instance (88, Plate XIII, figs. 6 and 7) figured slender forms as *Brachyphyllum*, from which there is a real difficulty of separation, it not being wholly certain that the nodes seen to be characteristic of forms like those shown in Figures 73 (*n*, *n*) and 74 are either present in most Williamsoniæ or absent in all Brachyphylloideæ.

FIG. 74.—Williamsonian stem casts from Lyme Regis and from Brora, Sutherlandshire, Scotland. All $\times\frac{1}{3}$. (From Carruthers.)

These stems are closely associated with the *Williamsonia* fruits of the Yorkshire and Scottish coasts, India, and Mexico. They indicate relatively slender plants with the habitus of the most freely branched forms of *Cycas*, and the foliar bases are persistent, short whorls of leaf bases alternating with conspicuous internodes of scale-leaf bases. But here the closer resemblances to other cycads cease, since Williamsonian fruits must have been attached to such stems as well as to the much slenderer and even more freely bifurcate *Wielandiella*.

The four stems figured are called (left to right) *Bucklandia Milleriana*, *Yatesia gracilis*, and *Y. Joassiana*. The smaller (Lyme Regis) is in the British Museum and the others are Brora specimens in the Dunrobin Castle Museum. Compare with preceding figure.

Indeed, because of certain *Cordaites*-like characters common to both these groups, such difficulty of separation may even be expected to increase with the finding of new and more varied forms. However, setting anatomic characters aside, it would tax belief to now regard the node-bearing group of stems as mainly Brachyphylloid instead of Williamsonian, in which case leaves and fruits only of the latter type would uniformly accompany stems only of the former in such widely separated localities as the Yorkshire coast, India, and Mexico. Such anomalies of conservation and association may be possible, but appear improbable.

Regarding the nodes of laterally broadened and smaller scars alternant with the long internodes of large vertically elongate and keeled rhombic scars, several explanations may be offered. But it appears from *Wielandiella* (Vol. I, Fig. 12) and the Paris Museum stem with leaves attached (Fig. 64) that the long internodal spaces were occupied by scale-leaves, the old bases of which thus really form quite three-fourths of the thin armor. The general habitus is near that of *Cycas*, which fully explains why such stems have been hitherto regarded as Cycadacean.

CYCADOLEPIS.

To various organs of a scale-leaf character found more or less closely associated with Williamsonian fronds, Saporta gave the appropriate name *Cycadolepis*. Easily the most striking occurrence of these scales known is that in the El Consuelo section of Oaxaca, where the form shown in Figure 66 is found on the same slabs with the stem type of Figure 73 A. That the internodes of large scars in these and other Williamsonian stems are due to the excision of just such *Cycadolepis* scales is the only fair inference. It is true that such heavily ramentum-covered scales have not been found attached to the imprints or casts of Williamsonian stems. But as determined in earlier chapters, ramentum-covered scale leaves are a characteristic feature of *Cycadeoidea*. In the silicified series there must be every gradation from the normal foliage leaves down to the bud scales and hairy bracts, while the scale leaves must have been as subject to periderm excision as the pinnule-bearing fronds. It is, however, probable that in the smaller and more typical Williamsonia stems the scale leaves were of rather reduced size, even where leaving fairly large scars. In picturing the outer appearance of the more normal Williamsonian stem it will doubtless be safer to avoid too close a parallel with *Cycadeoidea*. But even the latter, when divested of its bark and attached leaf bases, that is to say, all structures exterior to the cambium, as in figure 73C, assumes ordinary stem proportions. One may readily imagine varying development of the extra-cambial region all the way from such abnormal forms down to types with bark as little conspicuous as in conifers.

STRUCTURE OF NODE-BEARING STEMS.

Thus far the only Williamsonian stems yielding structure are the Indian specimens from Amrapara, with the bases of *Ptilophyllum* fronds attached, first described in 1863 by Oldham and Morris. A careful elaboration of this material has only recently been carried out by (Miss) Bancroft (13). The stems are borne on porcellanous blocks along with numerous fronds, and are silicified, but with limited tissue differentiation. Nevertheless, by soaking the sections in immersion oil it was made possible to discern important histologic details.

In the first place, Miss Bancroft figures a very characteristic stem fragment 12 cm. long with 5 cm. internodes, and a diameter of little more than a centimeter, when crushing is allowed for. The scale-leaf scars, about 20 to the internode, alternate with about the same number of frond scars. The fronds were obviously of the microphyllous type and could not have differed essentially in either structure or form from the finely conserved associated fronds of *Ptilopyllum cutchense*, *P. acutifolium*, or *Dictyozamites falcatus*, the only types noted in the blocks studied. A somewhat larger stem about 4 cm. in diameter and thus comparable in size with the stems found so closely associated with Williamsonian buds in India and Mexico yielded structural details. This is evidently the same type as the associated segments of stems which have the *Ptilopyllum cutchense* fronds directly attached, as figured by Seward several years since (279, p. 194). Miss Bancroft says of the wood structure and larger features:

"This stem possesses characters some of which are cycadeoidean, while others point to contact with the recent Cycads. The endarch nature of the xylem is common to all Cycadophytan stems, but the single compact woody zone with its narrow medullary rays is a characteristic feature of the cycadeoidean stems, wholly different from the looser structure of recent cycadean wood, formed in certain cases from successive cambiums. The Indian stem has multiseriately pitted tracheides similar to those of Cycads, as contrasted with the scalariform type usually occurring in the Cycadeoideæ. Like these, however, it has numerous secretory sacs in its parenchymous ground-tissues, rather than the gum-canals of recent Cycads. So far as external characters are concerned, the stem described resembles that of a recent 'armoured' Cycad in general appearance, for the leaf-bases, unlike those of the Cycadeoideæ, do not possess axillary structures; while in place of the ramental scales figured by Wieland for his American Cycadeoideæ, and by Seward for the English type *Cycadeoidea gigantea*, the leaf-bases are separated by a packing of ramental hairs."

These structures are in large degree significant. It should be observed, however, that such stems, if not themselves branched, are related to branched forms, and that the axillary buds of *Cycadeoidea* are essentially branches also found profusely developed in *Macrozamia* (64). There can be no question, however, that the hiatus between the stem habitus of *Cycas* and that of the Cycadeoids is here completely bridged. With regard to the wood structure let it be noted that the scalariform tracheides of *Cycadeoidea* may not be such a constant feature; pitted tracheides are conspicuous in *Cycadeoidea micromyela*, and there is a gradation from pitted to scalariform types in most instances, *C. Dartoni*, *C. Niedzwiedskii*, etc. Also, because of the faint color differentiation of the wood, there would be difficulty in seeing the scalariform markings which may be present. If pitted tracheides are actually more developed than in *Cycadeoidea* some nearer approach to Araucarians as well as existing cycads is indicated.

It is especially interesting to find that the ramentum here reaches a stage of reduction to filaments, as in existing cycads. Seeing that in *Dion* there are *Araucaria*-like growth rings as in *Cycadeoidea*, it becomes more obvious that vegetatively speaking the line of demarkation between the Cycadaceæ and the Cycadeoideæ has been largely swept away.

Regarding the comparative development of cycadeoid wood zones a word may be added. In the Cycadeoideas preservation very rarely extends to the base of the trunk, where in all cases the wood zone must be relatively heavy at the root insertion. The stem figured in Plate 5, photographs 5, 6, illustrates this feature. The basal section must lie near the level of the highest roots. In some trunks, however, the wood zone retains a heavy development at a considerable height. The *Williamsonia* stems, which are far longer relatively to diameter than any *Cycadeoidea* trunks whatever, therefore have much the greater wood development.

From the foregoing exposition of stem structure it may be fairly concluded that the wood of the Cycadeoidean [and Williamsonian] stems was at times, even in the more robust types, not only as heavy as that of *Cordaites*, but exhibited the same compact structure; thus permitting the open habitus of plants with small, freely branching stems, thin cortex, and finally excision or non-retention of old leaf bases, as in the conifers. And from this notable approximation of *Cycadeoidea* to *Cordaites*, taken with the known occurrence of small-stemmed forms and the even more significant complementary fact that following the seed-fern stem types of the Paleozoic there is that long series of Medullosan stems, it may be deemed virtually proven that the Williamsonian stem had, as a rule, a fairly compact wood zone and that it was normally slender and branching, and in the smaller, thin-barked, armorless forms could very readily be mistaken for coniferous types. At least it may be expected that when the discovery of a more extended series of Williamsonian stems does

finally come, solid types of wood, even those with annual rings, rather than the lax lattice of collateral bundles of the Cycadaceæ, and most Cycadeoideæ will prove abundant. It is becoming evident enough that instead of being representative of the Cycad vegetation of the past, these robust stems with thin wood, an immense medulla, and heavy, persistent armor, are exceptional to the point of abnormality. They do not represent the characteristic type of cycad vegetation in the past, which is reason enough for their relatively rare occurrence in ancient rocks; but it is equally clear that further progress in the study of the Williamsonian stems stubbornly awaits the discovery of carbonized forms of the lesser branching types, to which may be applied the staining and embedding methods so successfully introduced by Hollick and Jeffrey in their study of the Kreischerville conifers. Fortunately there is much reason to anticipate the finding of carbonized material favoring structural study in the Consuelo and other sections in the Lias of Oaxaca.

EARLY DESCRIBED OVULATE CONES AND BUDS.

Williamsonia (Podocarya) Bucklandi Saporta.

The first Cycadeoidean or Williamsonian fruit ever figured appears to have been Buckland's *Podocarya* of 1836 (42) from the "lower region of the inferior oölite," near Bristol, to the east of Charmouth, Dorset, on the coast near Lyme Regis. This petrified ovulate cone, "about the size of a large orange," was found by a Mr. Page of Bishport and transferred to the Oxford Museum, being subsequently lost to view. The loss of such a historic type is only less to be lamented than the failure of the locality to yield other recorded specimens; for a close study of Buckland's Bridgewater Treatise figures, as much later redrawn by Saporta in the form reproduced in excellent style on Plate XLVII, figures 5–8, Volume I, indicates a remarkable type of conservation.

As any one who has studied such fossils can easily see, all the figures have excellence stamped upon them. In particular the form of the seed and position and size of the embryo are clearly disclosed. The seed, "about the size of a small grain of rice," is slightly more angular than in other Cycadeoideæ, showing a distinctly pentagonal to hexagonal form with a rather clearly marked shoulder surmounted by five to six ribs of the blow-off layer. Even the minor details of the several figures are so obviously exact that from them a perfect model of the seed form could readily be constructed. While the "two lunate bodies" of the upper middle transverse section (see Buckland's original plate 63, fig. 7) are, of course, none other than the two cotyledons of a notably smaller embryo than is found in any *Cycadeoidea*. Evidently the seed had a well-developed albumen surrounding the embryo, an interesting point which leads to a suspicion that this may well be some Williamsonian form. Just once in his plate legends Buckland refers to the seeds as calcified, with the lunate bodies [embryos] dark; but from the remarkable conservation of the isolated specimen, it is likely to have been silicified, such fossils often having a whitish exterior, that without further test could deceive even a practiced eye.

There can be no question that in its entire structure the "Podocarya" parallels the *Cycadeoidea* and *Williamsonia* cones. The arrangement of seed stems and interseminal scales must be the same in both. The parenchymatous cushion is of the robust inverted pear type, and in form exactly intermediate between that of the *C. dacotensis* strobilus of figure 100, Volume I, and the *Williamsonia* of Plate XLVI, figure 1 (Vol. I). There is therefore no reason why this fossil should not be provisionally referred to the genus *Williamsonia*, with the suggestion that the small size of the embryo is a significant feature. The large size of the cone, even equaling that of the smallest *Cycadeoidea* trunks, would readily permit silicification, after the fruit had dehisced.

As in the case of the Isle of Portland Cycadeoideas, Buckland again advised with the great botanist Robert Brown as to the probable relationships of the new type of cone. As he explains the comparison intended:

"The spherical fruit of Pandanus is divided into many drupes. * * * The drupes contain from two to fourteen cells; and each cell when not barren contains a single oblong seed. The seeds within each drupe of Pandanus are enclosed in a hard nut. These nuts are wanting in the Podocarya, whose seeds are smaller than those of Pandaneæ, and not collected in drupes, but dispersed uniformly in single cells over the entire circumference of the fruit. The collection of seeds into drupes surrounded by a hard nut, in the fruit of Pandanus, forms the essential difference between this genus and our new genus, Podocarya."

The interesting point here is that neither Buckland nor Brown appreciated how far the parallel with Pandanus really extended! They could not know that a series of sterile interseminal scales surrounded the dicotyledonous seed in their fossil; they could not know that even to this hour the best explanation of the interseminal scales is that they are aborted organs essentially homologous to the fertile sporophyll which they inclosed. It is by no means impossible that the original comparison with Pandanus may yet be found to have some definite significance. That Saporta did not entirely dismiss it when later founding his proangiospermous group is equally interesting, as he also could not have understood the full extent of the parallel between the Pandanus drupes and the interlocking rosettes.

Williamsonia scotica Seward.

Over sixty years ago Hugh Miller assiduously collected the Liassic and Oölite petrifications and imprints of the Sutherland coast of Scotland in the neighborhood of Helmsdale and Eathie. That this region must vie with the Yorkshire coast in the abundance and interest of its fossil plants was long quite evident from the descriptions given in the "Testimony of the Rocks," and is fully confirmed by the recent memoirs of Seward (284, 287, 292). But the fact of especial interest here is that the figure 138 in the "Testimony of the Rocks" follows the "Podocarya" as the second illustration of a Williamsonian strobilus, both in point of time and importance; while the close association with Cycadeous fronds is definitely noted. The excellent illustration from the "Testimony of the Rocks" is repeated in Figure 75 D in about two-thirds the size of the original strobilus, which is silicified. Hugh Miller notes this fossil as follows:

"With the leaves of the Eathie Zamia, we find, in this northern outlier of the Lias, cones of a peculiar form, which, like the leaves themselves, are still unfigured and undescribed, and some of which could scarce have belonged to any coniferous tree. In one of these (fig. 138) the ligneous bracts or scales, narrow and long, and gradually tapering till they assume nearly the awl-shaped form, cluster out thick from the base and middle portions of the cone, and, like the involucral appendages of the hazel-nut or the sepals of the yet unfolded rose-bud, sweep gracefully upwards to the top, where they present at their margins minute denticulations. In another species the bracts are broader, thinner and more leaf-like: they rise, too, more from the base of the cone, and less from its middle portions; so that the whole must have resembled an enormous bud, with strong woody scales, some of which extended from base to apex. The first described of these two species seems to have been more decidedly a *cone* than the other; but it is probable that they were both connecting links between such leathern seed-bearing flowers as we find developed in *Cycas revoluta*, and such seed-bearing cones as we find exemplified in *Zamia pungens*. The bud-like cone, however, does not seem to have been that of a Cycadaceous plant, as it occupied evidently not a terminal position on the plant that bore it, like the cones of Zamia or the flowers of Cycas, but a lateral one, like the lateral flowers of some of the Cactus tribe."

An admirable account of the structure of the Eathie strobilus has recently been given by Seward (287). His figures indicate a close similarity in general form, size, structure, and development to the young *Cycadeoidea* strobili of Figures 90, 91, Volume I. As in those strobili, the seeds are small and little developed. In so deciding, it is, however, quite

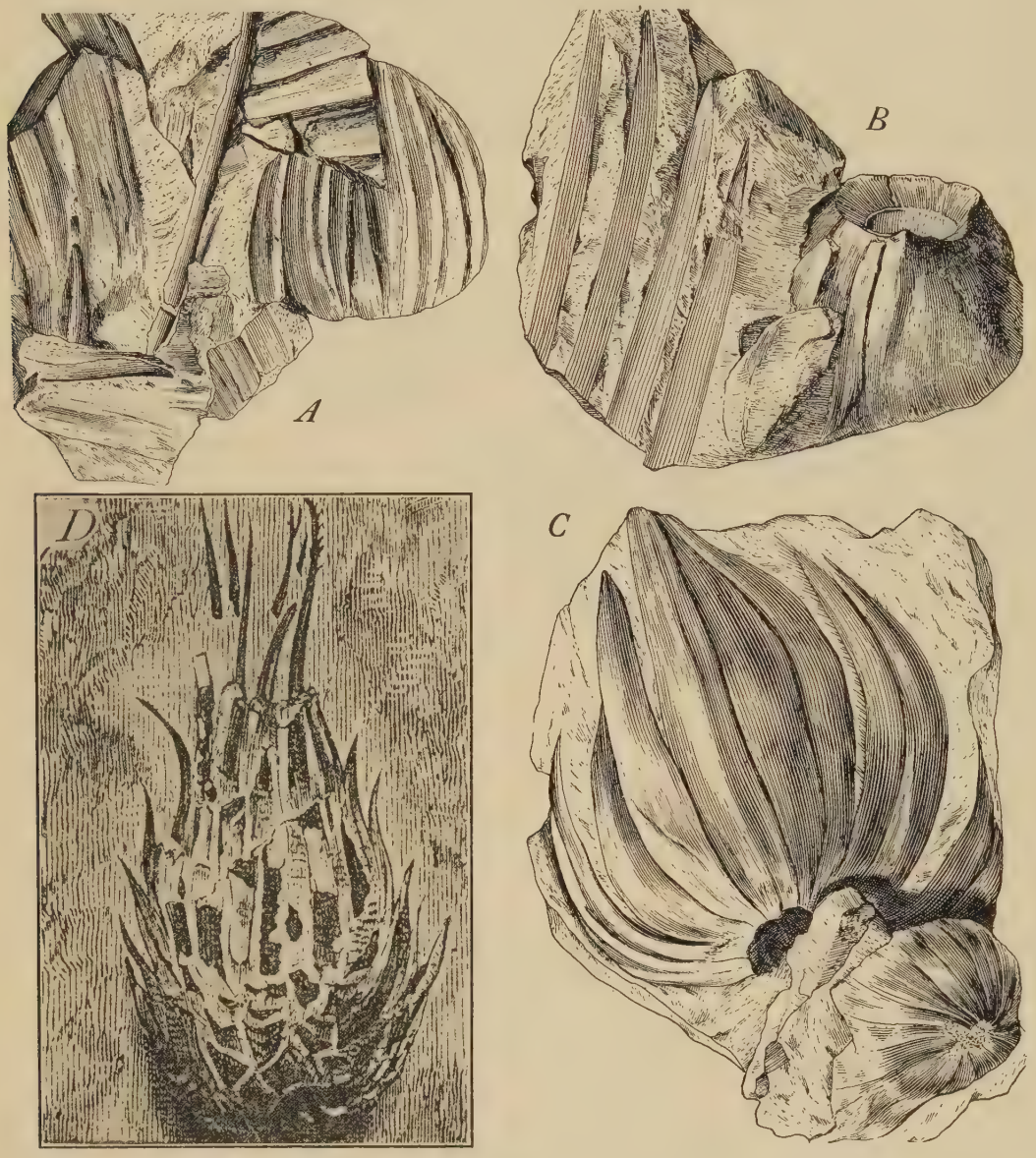


FIG. 75.—Williamsonian strobilar casts from Yorkshire (A–C), and the silicified strobilus from Eathie, Sutherlandshire, Scotland, figured by Hugh Miller, Testimony of the Rocks, p. 483.

A, B. *Williamsonia gigas*. ×½. Two views of partly conserved cast of bract-inclosed ovulate strobilus projecting from matrix traversed by many fronds of *Zamites gigas*, fruit and foliage. (Yale, James Yates Coll.)

C. *Williamsonia gigas*. ×½. Bract-inclosed strobilar casts probably borne on one and the same plant and further illustrating sharp outlines of these fossils and their great abundance. (Yale, James Yates Coll.)

D. *Williamsonia scotica*, the silicified Eathie seed cone. ×½. (*Cf.* p. 192.)

necessary to avoid being overinfluenced by the size of the seeds in the *Williamsonia Bucklandi* and other forms. There is no reason why these seeds can not have been minute; the micropylar tubes are, though so small, well developed, with structure quite comparable to that of older *Cycadeoidea* seeds; also, the nucellus is filled with elongate-celled tissue, very

possibly homologous to that seen in *Gnetum* as the archegonia begin to form. The most that can be said is that a pre-archegonial stage is indicated.

The parenchymatous cushion is not sharply conical and the sections cut do not disclose a basal disk shoulder. The condition at the base of the cone probably resembled that seen in figure 11 D. The surface characters of the cone are very similar to those seen in various younger cones of *Cycadeoidea*, in particular that of Plate XXIII (phot. 2), Volume I. The "bract denticulations" have the form of undeveloped pinnules and there is no direct suspicion that they are immature microsporophylls. The transverse sections show the bracts to be slender just above their insertion, but thicker in the mid-region. They are thickly

FIG. 76.—*Williamsonia* fructifications of the James Yates collections from Cliffs of Hawkser and Runswick (1843 or before). $\times\frac{1}{2}$ nearly.

A. *Williamsonia* (species). Probably not *W. gigas*, the bracts or scale leaves being very large. This specimen is in the collections of the Jardin des Plantes, Paris. It is figured by Saporta in Plantes Jurassiques. The present figure results from developing the specimen slightly. Two views of the terminal bud are given.

B. *Williamsonia gigas* fruits and foliage, accompanied by large and broad leaf of *Yuccites* (=*Cordaites* ?). (Yale, James Yates Collection.)

beset by fine hairs, not the ramental scales so uniformly found in *Cycadeoidea*, which at times approach a thread-like form. This feature, however, recalls the similar reduction found in the ramentum of the Indian Williamsonian stems. As in *Cycadeoidea* there is a heavy development of sclerous scalariform hypoderm forming the upper half of the bract ground-mass.

Only the sections reveal the presence of a small lateral bud borne below the base of the cone nearly at a right angle to the stock. The presence of this bud of course suggests renewed vegetative growth of the axis following fructification, and reference to some typical Williamsonian stem rather than to the robust Cycadeoidean type. It is, as Seward says, difficult to declare that the type is strictly Williamsonian; but his opinion that the

"*pis aller* of a new genus" is here unnecessary must at once find consent. The boundaries of a fossil genus are never certain, and never settled. It is possible that the *Williamsonia scotica* was derived from an armor fragment; but this is the least likely alternative and, with the prosecution of further field work on the Scottish coast, confirmation of a Williamsonian relationship may be anticipated. No further mention of the second "enormous" laterally borne bract inclosed axis mentioned in the "Testimony of the Rocks" is recorded, and other specimens have not been recovered. The type must be like that of Figure 77.

Progress in the investigation of Williamsonian strobili was not destined to be made directly from the two remarkable examples first discovered, the mature "Podocarya" and the immature Eathie form. It is therefore necessary to turn back to the Yorkshire coast series.

YORKSHIRE COAST STROBILI.

The discovery of the Williamsonian tribe may be fairly said to begin early in the last century with the collection of the sightly buds, ovulate fruits, disks, and leaves of *Williamsonia gigas*, found intermingled with an abundance of other fossil plants along the eroded cliffs of the Yorkshire coast. Here Williamson and his father, as well as other local collectors, diligently sought out the handsome series of Cycadophytan fruits, which mostly found their way into the Williamson collections and those of the Jermyn Street Museum, of Cambridge, and the James Yates collection. Williamson says that his father first drew attention in 1832 to some fine specimens he had just discovered at Hawkser, both visiting the locality in 1833 (402). But it appears that the partly indiscriminate search for "*Pracht-Stücke*" had mostly ended by 1835 or 1840 without the careful establishment of quarries, and without attention having been directed to the abundant and important smaller fruits and disks of other species of *Williamsonia*, which the visits of Nathorst, first in 1879 and then in 1907, followed by that of his associate, Halle, have brought to light. So that for quite thirty years previous to the study of *Cycadeoidea*, which again so pointedly directed attention to the Yorkshire coast fossils, the original and more or less scattered collections of Williamsonian fruits failed of addition and came to be regarded as rarities; the more especially so after Saporta's view that the ovulate cones were *Pandanus*-like, just as Buckland originally surmised in the Bridgewater Treatises. Indeed, the later discovery of similar cones in close association with the *Ptilophyllum* leaves of the Gondwanas, and Nathorst's observation of related fruits with *Anomozamites* leaves, would almost seem to have confirmed any ideas of isolation and rarity of such fruits, or even to have diverted attention from the urgent need of renewed study in nearer fields. And it still remains difficult to understand why most of the localities of Mesozoic fossil cycads indicated on the map (Figure 89) have so far failed to yield other than scattered fruits. In truth, it has required not only the renewed field work on the Yorkshire coast, but the *richesse* of Williamsonian fruits in the newly discovered Mexican horizons to fully and finally dispel this mistaken idea of the rarity of casts, imprints, and fruits, and especially of difficulty in learning the import of the main facts of association.

SEED-CONE STRUCTURE.

The Yorkshire coast strobili include two main types of preservation. The first is an uncrushed type more properly described as a structureless cast. In these uncompressed casts preservation is wholly capricious and may end at any point. In no case are the seeds actually conserved; but this fact must be due in part to the splitting away of the seed zone. While, however, the seeds fail to outline themselves, the parenchymatous cushion is often

well outlined and the conserved interseminal scales are very apt to clearly demark the fruit base and the summit, a caprice of cast and imprint formation also much in evidence in the Oaxacan region. (See Fig. 79.)

The second type of ovulate cone is more distinctly carbonized and generally crushed out flat. The first example of this character to be noted was the *Williamsonia Leckenbyi* from Cloughton Wyke, a rather large form discovered by Nathorst in 1879 (186). But it was not until much more recently that Nathorst (194, 197) described several characteristic lesser forms of the crushed-out carbonized species, which are freely accompanied by the staminate disks called *Williamsonia spectabilis* and *W. whitbyensis*.

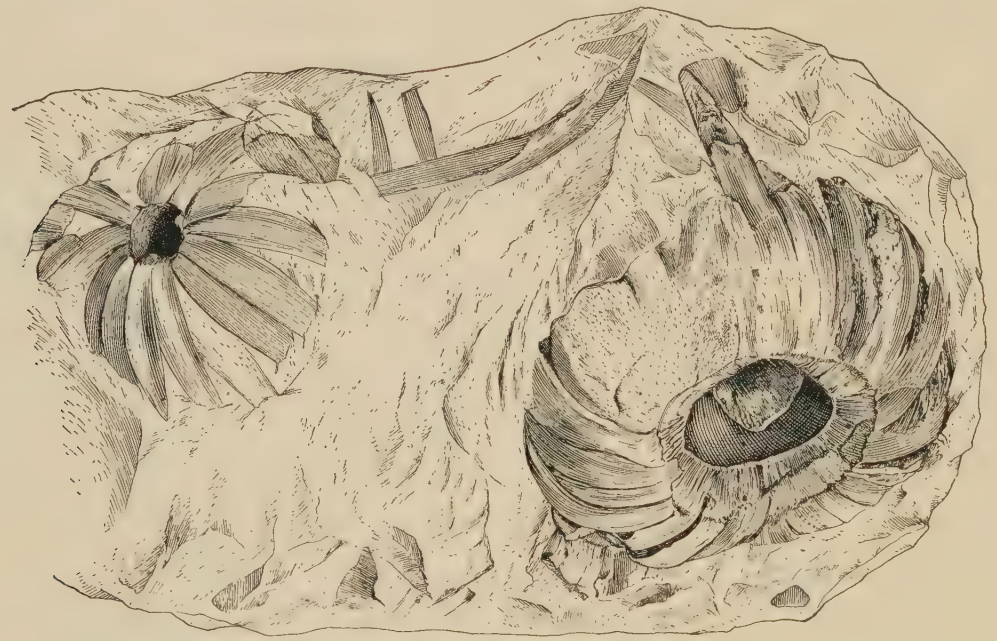


FIG. 77.—*Williamsonia gigas*. Slab bearing foliage and two fruit casts weathered out in nearly full relief. The ovulate fruit to the right is of the largest size and the sterile scales of the base are quite distinct. Yorkshire coast Liassic of Hawkser and Runswick. (Yale, James Yates Coll.) $\times \frac{1}{2}$.

The ovulate fruits collected in the early days, when the naturally weathered-out specimens were to be found in some abundance, are the large forms 5 to 8 cm. in diameter, and often but not always flattened. Such are shown in the painstaking drawings of Mr. R. Weber, reproduced in the Figures 75–78, all the result of joint study of details by both writer and artist. These specimens are all from the James Yates collection, secured for the Jardin des Plantes by Brongniart, 1843. A portion of this collection is now in the Yale Museum; and from this series the figures are taken, with the exception of Figure 76 A, which is a type retained by the Jardin des Plantes.

The striking association of fronds with an abundance of strobili in some of the weathered specimens seemingly broken up at random, appears especially in Figure 75, A, B. But further considering fruit outlines, a most instructive strobilus is fully illustrated in complete projection by Figure 78, showing the lateral and end views, with a median longitudinal section partly restored. As clearly appears from the figure, the bracts inclosed a strikingly handsome fruit; though, as partly due to weathering and partly to the lack of uniformity in preservation, no surface details actually appear, and one is left to wonder at the weathering-out so nearly on the original outer surface. But, contrariwise, certain interior features

are unexpectedly found; the form of the conical-shaped receptacular axis is sharply outlined, some of the soft tissue even retaining structure; while at the apex conservation again begins in the outcurving mass of interseminal scales, and as sharply ends to form a pyriform cavity more or less filled with the white clayey material "scarbroite." In fact, we can easily see that the entire space occupied by the cavity was in life filled out by the continuation of the zone of slender sterile organs as a closely packed mass, silky or wavy and slightly spreading at the summit.

FIG. 78.—*Williamsonia gigas.* ×⅔. Ovulate strobilus of the Yale-James Yates collection from the cliffs of Hawkser and Runswick (1843 or before).

A. Lateral view showing, together with portions of ensheathing husk of bracts, apical cavity due to failure of conservation resulting in "pyriform" surfaces.

B. Basal view showing large peduncle scar, and somewhat worn surface of strobilus, with bracts split off or worn away.

C. Apical view, nearly the same as A

D. Partial restoration of cone effected by sawing in two, and drawing in natural form and position the seed stem and seed zone which failed of conservation, though the axis is fairly conserved. (Hence restored view = median long. section.)—*The strobilus probably ended as a loosely compacted and flowing more or less silky mass of sterile filaments, just as in Cycadeoidea dacotensis.*

Throughout the entire fruit, therefore, the manner of preservation is found most instructive in its bearing on both fossilization and features, it being altogether clear how preservation of the sterile apical region with either dehiscence of the lateral mass of seed stems and interseminal scales, or its non-preservation, would at once result in the formation

of the "pyriform axes" figured by Williamson and so puzzling in his day. In addition to the suggested early dehiscence of the seed-stem zone, its preservation as a weak zone easily split off during erosion may also account for some of the axes figured by Saporta.

However this may be, in the present case the finely outlined form suggested that the strobilus was a complete one at the time of fossilization, and it was hoped that a longitudinal section might reveal inner features. But on sawing through the fruit longitudinally, and smoothing the surface of the saw cuts, all directly visible traces of the internal structure outside the conical receptacle were found curiously absent.

So too in the case of the huge bud reproduced in only half the natural size in figure 77, a saw-cut only disclosed some lesser apical detail. In both instances it seems that aside from the condition of the fruit at the time of fossilization, the indication of tissue zones has been partly determined by the course of erosion and weathering from the matrix. Curiously enough, the parenchyma ground-tissue of the receptacle is well enough conserved to plainly show the gum canals, whence the outer zone may be restored with all confidence, as has been done in outline in figure 78 *D*; and it would be likewise exact to represent the apical region as a long and finally spreading top of sterile scales. In fact, it is marvelous to find first one and then another feature conserved until, not forgetting the supposed "Podocarya" of Buckland, it is clear that had all the evidence been rigidly put together, a fair reconstruction of the entire fruit and form of fructification could have been made long before the later discovery of the silicified specimens.

It should be added that the fructifications of the Yale series shown in the adjacent figures are but a small portion of the original James Yates collection. That still reposed in the Jardin des Plantes includes a wealth of fruits of the type shown, and there can be no question that further illustration would prove very interesting.

OAXACAN STROBILI.

Following early discoveries along the Yorkshire coast, the Jurassic strata of other parts of the world have from time to time yielded Cycadeoid cones more or less sparingly. Small but interesting collections have been made in Sardinia (134), larger ones in the Lunz of Austria (133), and especially in the Rajmahal Hills of India (86); while a considerable list of isolated "finds" (Virginia, Oregon, etc.) might be cited. But no horizon hitherto found surpasses the Oaxacan Lias of Mexico, because of the possibilities of collection and the varied series of Williamsonian cones already recovered. This region and its interesting fossil plants was first brought to notice by the writer. His results have been published in papers preparatory to the present volume (391, 394), and in a memoir on the Liassic Flora of the Mixteca Alta (396).

The Mixteca Alta is a portion of the southern border region of the Cordilleran system, facing the Pacific and extending through central and western Oaxaca well into Guerrero and northerly into Puebla. It is not in the main a markedly elevated portion of the so-called high plateau region of Mexico; to the north rise the lofty peaks about Puebla and to the southeast the great Sierra Juarez mountain knot, the latter resting almost directly on the Cordilleran front. The upper Mixtecan region in which the Jurassic plant-beds are a great geologic feature is in part a moderately elevated but much folded and faulted basin. Or at least there are border or transverse ranges which have partially protected both the marine and underlying fresh-water deposits from the full effects of dissection and erosion, from all those tremendous tectonics to which the superbly picturesque Mixteca Alta region has long been subjected.

The ten or twelve thousand feet of Mesozoic strata which give character to the Mixteca Alta are about equally divided between the Jura and Cretaceous, any Trias that may occur not being as yet distinctly classified. The Mesozoic mass is often entirely freed from Tertiary eruptives, ash, or conglomerates, and rests on older sedimentaries of undetermined age, or against intrusives. The topography is exceedingly rough. The streams in cutting through the massive Cretaceous limestones capping Jurassic strata of lesser induration form a tremendous system of deeply cut valleys, gorges, and cañons. Yet because of the distinctly varied vegetation and rather free growth of pine and oak, with relatively few barren stretches, scenic aspects are far softer than in the upland mountain country of central Mexico.

As one sees by reference to the map, Figure 87, this region lies in exactly the same latitude on the opposite side of the globe from the Rajmahal Hills. Its geographic position is thus impressive, while the flora and all the advantages of an unsurpassed climate render it at once the most attractive and promising of all regions for the collection of Cycadeoid fruits. It is therefore most important to record the localities yielding early Mesozoic plants. Those which follow must be but a small portion of the localities where Williamsonian fruits and foliage may yet be found in abundance.

1. On the Tlaxiaco River to the westward of the town of Tlaxiaco at prospects of the Oaxaca Iron and Coal Company.
2. In the hills 3 to 5 kilometers northwesterly from Tlaxiaco.
3. At Mixtepec on the Rio Mixtepec, where considerable prospecting for coal has been carried on.
4. About and to the east of the Cerro del Lucero in the Tezoatlan and Rosario region.
5. On the Barranca Consuelo between the Cerro del Lucero and Cerro del Venado. Here a magnificently exposed section permitted the location of various quarries and the accurate measurement of plant-beds reaching nearly 600 meters in thickness. In addition, the prospects of the Oaxaca Iron and Coal Company, where some coal is actually mined, made possible collections from the lower third of the section which could hardly have been had from the surface quarries alone.
6. Near the prominence called "Piña de Ayuquila" near the village of Ayuquililla, in the State of Puebla. A fruit locality.
7. In light-colored, porcellanous (?) shales (doubtless comparable to the *Ptilophyllum* trunk-yielding shales of the Rajmahal series) observed near Tlapa, in the State of Guerrero. A fruit locality.
8. Near Huachenango, and elsewhere in the State of Puebla.
9. In the valley of the Nochixtlan River to the southeast of Chalcotongo; plant-beds 400 meters in thickness, perhaps equivalent to the Sonoran Trias. Probably a Triassic extension of the Barranca Consuelo section.

These Cycadeoid-yielding localities must represent a series of horizons extending from perhaps typical Triassic strata through the Rhætic and Lias. At No. 5 the cañon of the Rio Consuelo cuts through plant-beds 2,000 feet in thickness. Here a profusion of Williamsonian fruits is to be found, varying in size from small forms but a centimeter in diameter up to the larger types. The fruits are frequently carbonized and represent, apparently, a considerable number of species, although not so varied in form as the accompanying frond species. The occurrence of ovulate fruits and fronds in the beds exposed along the Rio Consuelo is, so far as yet determined, the following:

Occurrence of Cycadeoids in the Rio Consuelo section, Oaxaca.

Lower 250 meters.	Upper 300 meters.
Anomozamites cf. *Lindleyanus.*	*Cycadeospermum oaxacense.*
Otozamites hespera.	*Cycadolepis mexicana.*
Otozamites hespera var. *intermedius.*	*Otozamites cardiopteriodes.*
Otozamites Mandelslohi.	*Otozamites hespera* var. *latifolius.*
Otozamites Molinianus.	*Otozamites Reglei* var. *lucerensis.*
Otozamites paratypus.	*Otozamites (Williamsonia) Aguilariana.*
Otozamites obtusus var. *Liassicus.*	*Otozamites (Williamsonia) Diazii.*
Otozamites obtusus var. *oaxacensis.*	*Otozamites (Williamsonia) Juarezii.*
Otozamites (Otopteris) sp.	*Otozamites (Williamsonia) oaxacensis.*
Otozamites Reglei (variety).	*Ptilophyllum acutifolium* var. *maximum.*
Otozamites (Williamsonia) tribulosus.	*Ptilophyllum acutifolium* var. *minus.*
Pterophyllum cf. *contiguum.*	*Ptilophyllum pulcherrimum.*
Pterozamites (Pterophyllum) angustifolius.	*Pterophyllum Münsteri.*
Stangerites oaxacense.	
Williamsonia fructifications:	*Williamsonia* fructifications:
W. Huitzilopochtli.+stems.	*W. Centeotl.*
W. Nathorstii.	*W. Cuauhtemoc.*
W. Tlazolteotl.	*W. Ipalnemoani.*
W. Xipe.	*W. Mexicana.*♂
W. (species).	*W. Netzahualcoyotl.*
Zamites confusus [var.].	*W. Quetzalcoatl.*
Zamites Rolkeri (Puebla occurrence).	*W. Texcatzoncatzl.*
Araucarioxylon mexicanum.	*W. Tlazolteotl.*
Noeggerathiopsis Hislopi.	*W. Xicotencatl.*
Trigonocarpus oaxacense.	(Williamsonian stems.)

Characteristic ovulate cones from the Rio Consuelo section are shown in figures 79 and 80. The *Williamsonia Nathorstii*, the cast of which is shown at Figure 79 *c* is a natural mold. This species is in size and general form more like that of the lost Oxford "Podocarya" or *Williamsonia Bucklandi* than any other known form. The presence of a slightly conical apex of sterile organs, quite in agreement with other Williamsonians, appears to be the only difference from the Buckland strobilus, which, so far as one may judge from the figure, had the apex all fertile.

The Figure 79 *d* shows the mold or impression of the basal surface of a cone, with the peduncular insertion. At 79 *e*, is shown the carbonized outer surface of the mid-region of a fruit where yet made up mainly of sterile scale heads; though a few micropylar tubes may be seen. The figure is enlarged three times.

Figures 79, *a* and *b*, show two ovulate-cone bases, the outer parts of which are carbonized. In *a* the carbonized layer is split off and displays the striations due to the interseminal scales and seed stems. In *b* the basal sterile carbonized husk is split out of the concavity on the lower side to expose the impression of the outer fruit surface formed by the polygonal scale ends. It is not quite clear why the interior portions of these fruits are not conserved, as somewhat flattened but quite completely carbonized fruits of several smaller species are also present. But the best explanation is that the forms *a* and *b* are basal husks left behind after the dehiscence of the interior mass of seed stems, precisely as in the common tulip tree *Liriodendron*, where such basal collars of sterile scales are a conspicuous sight in all the late fall and winter.

The drawings of figure 80 show very clearly the surface characters of the sterile basal husk, as well as the transition into the fertile zone. In none of the forms here figured from Oaxaca can it be definitely determined whether an hypogynous staminate disk was present

or not, although in the case of the Paris Museum cast, Figure 80D, a bisporangiate condition may be indicated if the part seen is from the apical region of the fruit. With regard to the specific series of Oaxacan cones it should be understood that the delimiting characters are mainly macroscopic; but there is every reason to believe that with the ultimate histo-

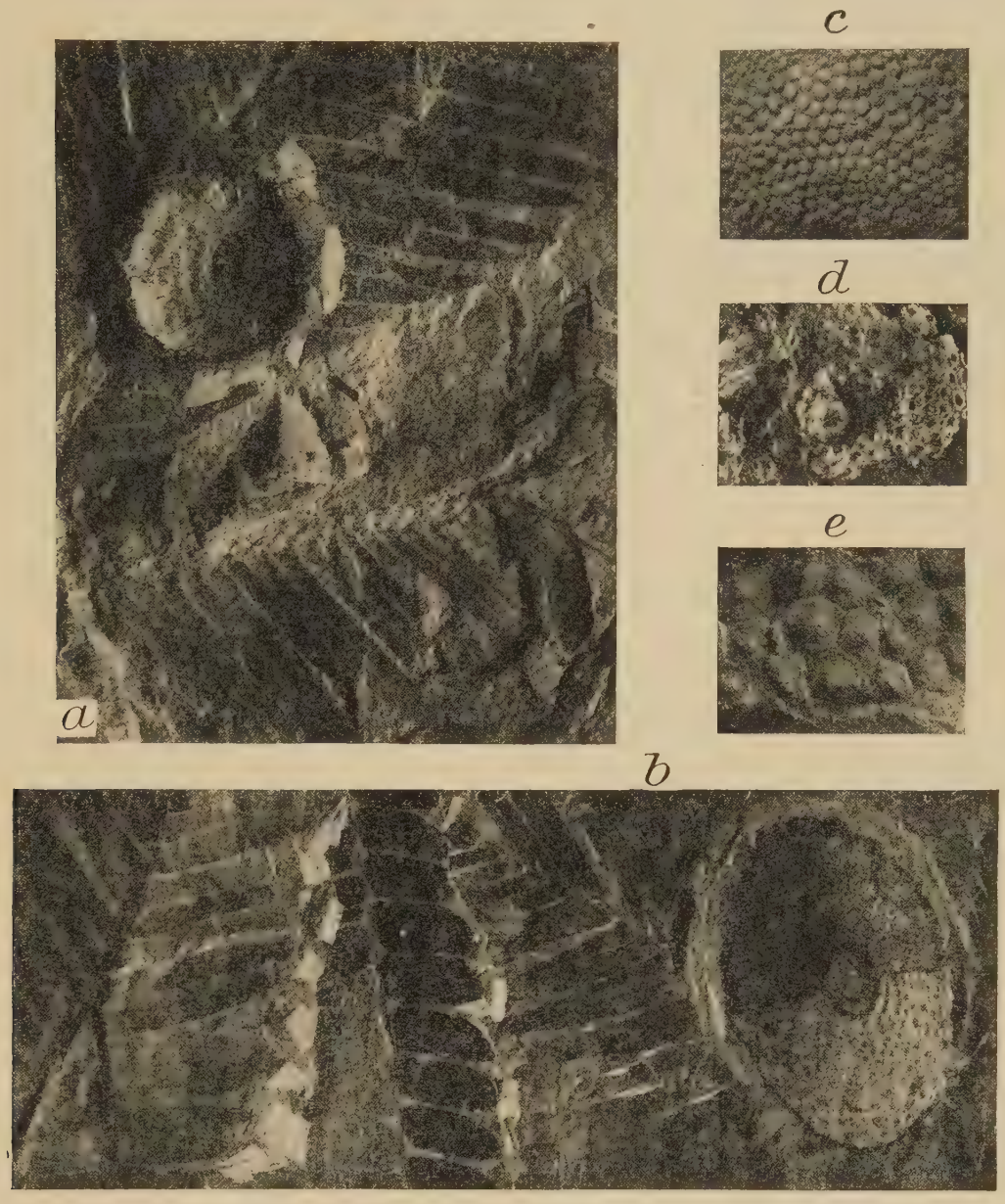


FIG. 79.—Liassic Williamsonias from the Rio Consuelo section of Mixteca Alta of Oaxaca, Mexico. The fruits and fronds of various species occur closely associated in abundance. All the figures are natural size, except *e*, which is enlarged three times.

a, d, b, e.—*Williamsonia Netzahualcoyotl* Wieland, with fronds of *Otozomites hespera* var. (slender pinnules), and *Otozamites Reglei*, var. *lucerensis*. The latter has the short, broad pinnules.
c.—*Williamsonia Nathorstii* Wieland. This is a clay cast from the original *fossil mold*.

logic study of the forms the presence of specific variety will be amply confirmed. That several different genera of fruits are also represented is nearly certain; for one can not believe that large bract inclosed strobili like that of figure 66 can belong to the same genus

as certain very small fruit buds with bracts of different form and long slender peduncles only a few millimeters in diameter. [The specific names of the Mexican fruits derived from the Aztecan mythology are facile to the Spanish spellings and serve to record locality.]

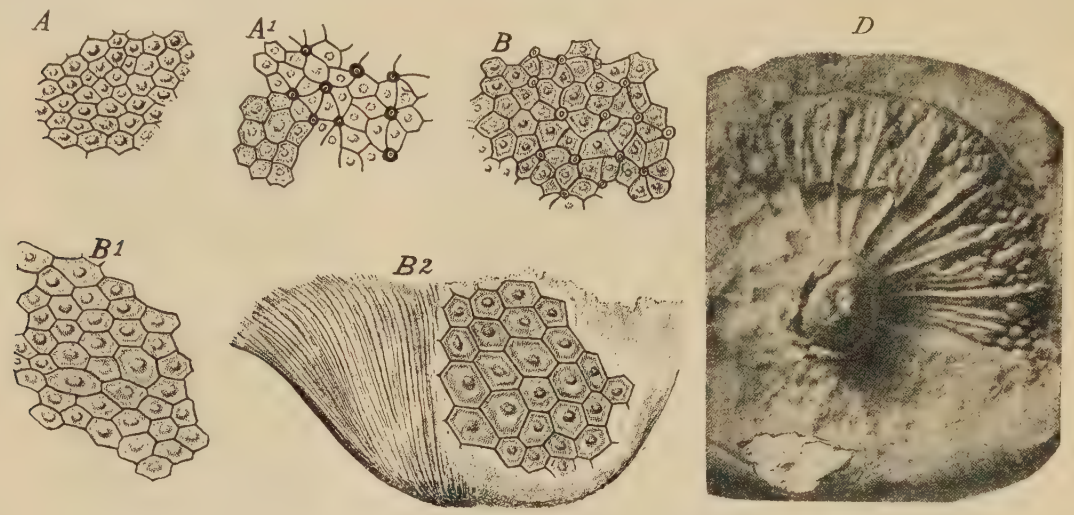


FIG. 80.—Surface features of Williamsonian fruit casts.

A–B¹. Outer surface of *W. Netzahualcoyotl* cones from the Rio Consuelo Liassic of Oaxaca, Mexico. ×$\frac{7}{4}$. A, sterile, A¹, B, partly sterile and partly fertile areas. B¹, B², an apparently different species from the preceding with large sterile scales occupying all the lower half of the fruit axis. In B² the outer nailhead-like ends of the scales have so split away as to reveal the stem mass beneath. The drawing shows all of the fruit conserved.

D. *Williamsonia* sp. ×$\frac{5}{8}$. Study of features of the cast (positive) of the original in Paris Museum, Yates Collection, No. 2406. Compare Figures 23–26.

STAMINATE FRUCTIFICATION.

It has been justly doubted by Professor Nathorst, to whom we owe the demonstration of the type series of staminate *Williamsonia* fruits from the Yorkshire coast, whether the nature of these pollen-bearing structures could have been satisfactorily deciphered before the elaboration of the silicified bisporangiate strobili of *Cycadeoidea*; for not only are the essential structures of the imprints of staminate organs difficult of observation, but the exigencies of preservation are greater by far than in the case of the ovulate cones. Indeed, because of the compact and durable form of the latter, with a requirement of several years for reaching maturity and shedding of the seeds, it might well be expected that, as in the Consuelo section, many seed cones must be found to one of the fragile staminate fruits of quicker growth, probably as a rule dehiscent only after the wilting down of their little-resistant tissues. Yet, evidence of staminate fructification has been accumulated with fair success, and, now that the outlines of the disks in a number of species and several genera are known, and the necessity for careful quarry work followed by approved laboratory methods is understood, we may not only hope to find better conserved disks and whorls of the types already sparingly observed, but those of hypothetical reduced forms. In fact, we even get the clearer suggestion of family differentiation in the more diffuse organs of the staminate series.

DISK STRUCTURE.

With the exception of *Wielandiella*, the principal known disk forms are illustrated in the plates of Volume I, and in text-figures of the present volume and Plate 56, together with the accompanying figures 80 D and 81. It is scarcely feasible to either restore or refigure the *Wielandiella* disk, evidently the most reduced form yet discovered. The 17 or 18

microsporophylls which compose the disk bear well-conserved pollen and appear to be reduced to the condition of mere heavy, blade-like, short stamens, basally fused into a shallow campanula in which is set a typical Williamsonian cone of medium to small size and rather rounded form. Much of the histologic structure is conserved and the original descriptions and plates of Professor Nathorst (189, 194) should be consulted. Taking stem habitus, foliage, and disk structure together, *Wielandiella* is separated from *Williamsonia* by more than the simple generic gap. Two related families of the Williamsonian tribe are indicated.

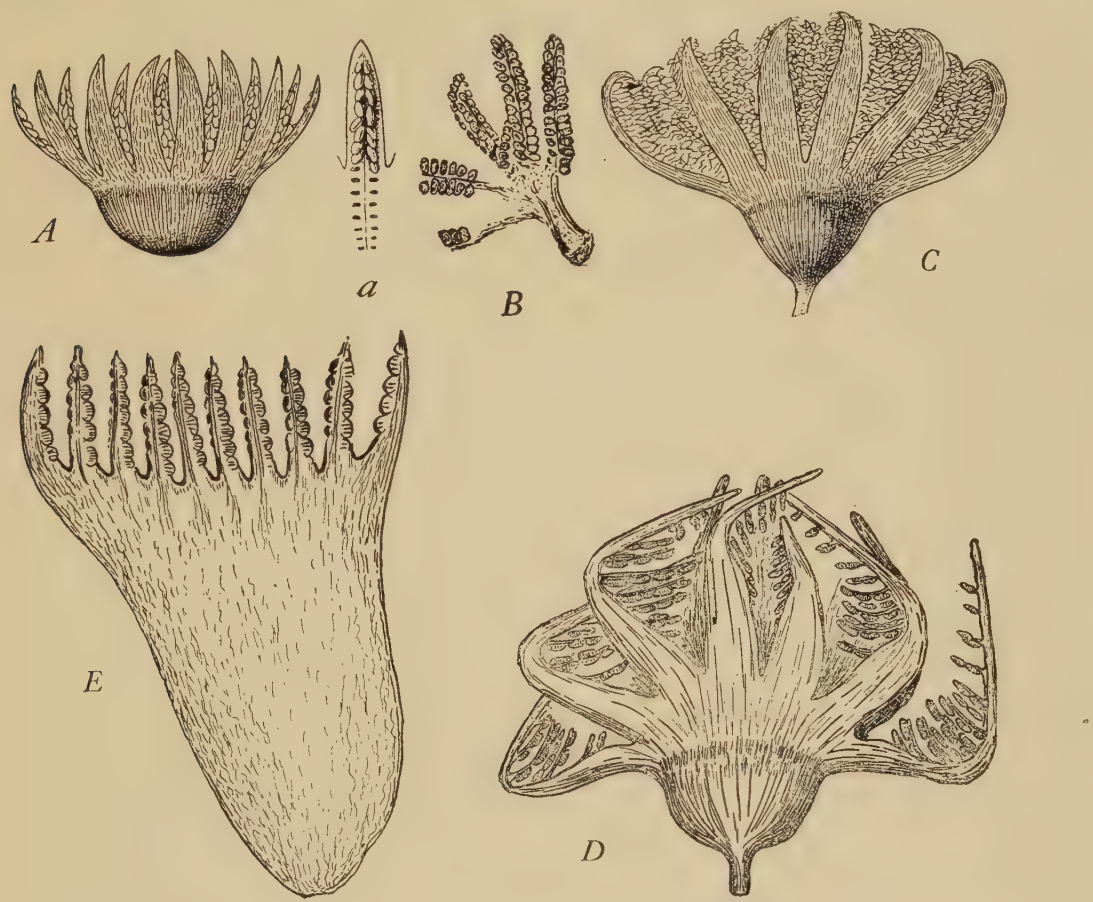


FIG. 81.—Five types of Williamsonian pollen-bearing organs.

A. *Williamsonia whitbyensis*. $\times\frac{1}{2}$. Yorkshire coast Liassic. As restored by Nathorst. (*a*) superior face of single pinnule with attached synangia.

B. *Williamsonia* (?) *rajmahalensis* (Wieland sp.). $\times 1$. After Feistmantel's figure of specimen from the Liassic of Bindrabun, Rajmahal Hills, India. Unisexual whorl. *Cf.* 88, p. 131, and pl. XXXIX, fig. 5, 5*a*.

C. *Williamsonia spectabilis*. $\times\frac{1}{2}$. Liassic of Yorkshire coast. As restored by Nathorst.

D. *Williamsonia spectabilis*. $\times\frac{2}{3}$. As restored by Hamshaw Thomas.

E. *Williamsonia mexicana* Wieland. Liassic of Oaxaca. Restoration, $\times\frac{3}{4}$.

Another distinctive type is the *Cycadocephalus Sewardi*, the outer form of which is shown in Volume I, Plate XLV, photograph 1. A painstaking restudy of this deeply interesting fructification, carried out by Professor Nathorst (194), has proven the correctness of the view advanced in Volume I that a staminate disk is present; but it appears that the fructification is unisexual, and that the pollen-bearing organs are of a peculiar elongate type very different from any Williamsonian synangium. Here again, a family-wide difference from other forms is indicated. (*Cf.* tabulation on page 205.)

Aside from the two foregoing staminate types, the form which has in recent years provoked the most discussion as to the floral type indicated is the as yet unique Paris Museum cast of a *Williamsonia* from the Yorkshire coast, shown at figure 80 D. The several explanations of this fossil advanced by Professor Lignier and the writer (*cf.* Lignier 144, 150, and Wieland 391, p. 463), do not require lengthy notice here. Since the discovery of the spurred condition of the *Cycadeoidea colossalis* disk with the symmetrical dome formed by the disk spurs, illustrated on Plate 56, it appears easier to explain this "litigious" cast. It is evidently from the apical synangial zone of a bisporangiate strobilus of the Cycadeoid type. The inner portion must represent the upper part of an elongate ovulate cone, adpressed to which are parts of the spurred staminate fronds. It is interesting to recall that Saporta believed the ovulate cone to be surmounted by some kind of leafy apex, perhaps like that shown on Plate XLVI (phot. 7), Volume I. That it is the disk which rises to form a circle of spurs was not suspected by anyone, owing, as it turns out, to the simple accident of uniform erosion or breaking away of such parts in most of the earlier studied axes.

The structure of the remaining disk forms is much simpler, and the several species, with the exception of the Rajmahal Hills form, figure 81 B, readily fall within the Williamsoniæ. The *Williamsonia mexicana*, figure 81 E, is one of the most interesting types because of its thin texture and the likelihood that it was shed entire just like the petaloid disks of some present-day tree types are shed in great numbers. The close parallel between the *Cycadeoidea* and *Williamsonia* staminate frond or disk component is further illustrated by Nathorst, who points out the general similarity to sterile fronds (199).

FLORAL TYPES.

Since the discovery of the bisporangiate flower-buds of *Cycadeoidea ingens* in 1899 and the interpretation of the true nature of the *Williamsonia gigas* fruits, just about an even score of staminate disks or whorls have been described. These certainly represent over 20 distinct species and several genera, possibly even more than one family. In most cases the exact form of the disk with the precise number of sporophylls is known. It is not absolutely certain that forms like *Williamsonia mexicana* are unisexual; but it seems that the form *Williamsonia* (?) *rajmahalensis* is, accurately speaking, a unisexual whorl of staminate fronds rather than a disk. The bisexuality of some Cycadeoideas is probable, but the *C. Jenneyana* was found to be monœcious; diœcism likewise being both possible and probable for some forms. The variety of forms already found is sufficient to indicate that the discovery and determination of structure of Williamsonian fruits is only fairly begun. Even so the series is cosmopolitan and impressive; for the forms persist throughout the entire Mesozoic and antedate the angiopserms in the most suggestive manner. The principal assigned Cycadeoidean and Williamsonian staminate types with the age in which they occur are given in the opposite table. The complementary ovulate series has the same geologic range. Taking the world over, about 35 well-marked species can be cited. It might be preferable to combine the ovulate and staminate groups in tabular form. But the structure of the ovulate series must be more diverse than can be readily proven; and as earlier remarked, it is easier to see variation in the staminate flowers. The simpler form of tabulation may therefore suffice, without at present appending a list of ovulate species.

It is as yet too early to attempt to divide the Williamsonian-Cycadeoid alliance into families on the basis of floral structure, even if the foliage and stems were not in the way. Too few facts bearing on the extent of sex differentiation have been accumulated; but a point has been reached where an initial grouping of types becomes desirable.

Staminate Whorl and Disk Species of Williamsonia and Related Forms. (Provisionally grouped.)

(*A*) *Cycadeoidea.*—Various species of bipinnate frond disks. Bisexual and monœcious or diœcious.

(*B*) *Cycadocephalus Sewardi* Nathorst.—Has tetrahedral fern-like microspores borne on large deeply cleft disk of 15± sporophylls. Unisexual. The type of an ancient family.

Weltrichia (?) *mirabilis* Fr. Br.—Disk 15-lobed.

(*C*) *Williamsonia spectabilis* Nathorst.—Disk 15± bipinnately parted fronds. Unisexual.

(*D*) *Williamsonia setosa* Nathorst.—Disk of 18± parted fronds.

Williamsonia whitbyensis Nathorst.—Disk pinnately 15-cleft.

Williamsonia pecten Nathorst.—Small disk form. Unisexual.

Williamsonia tuberculata and *bituberculata* Nathorst.—Disk pinnately 15-cleft.

Williamsonia mexicana (Wieland).—Disk pinnately 10 or more lobed. Unisexual (?).

(*E*) *Wielandiella angustifolia* Nathorst.—Disk or close-set whorl of small stamens. Bisexual.

Wielandiella punctata Nathorst.—Disk or close whorl of minute, nearly sessile stamens.

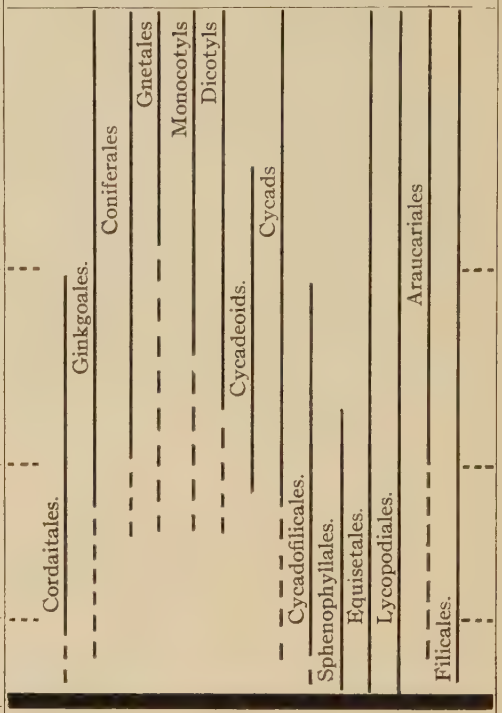
(*F*) *Williamsonia rajmahalensis* (Wieland sp.).—Short whorl of (6+) small elongate staminate scales or staminophylls. Unisexual.

Williamsonia (?) *Lignieri,* Nathorst.—Small, whorled, scale-like stamens.

Cycadeoid Staminate Flowers.

No.	Name.	Microsporophylls.	Age.
1	*Wielandiella angustifolia*	17 or 18	Rhaetic.
2	*punctata*	20±	Rhaetic.
3	*Cycadeoidea (Cycadella) wyomingensis*	13	Upper Jurassic.
4	*dacotensis*	18	Lower Cretaceous.
5	*etrusca*	.....	Lower Cretaceous.
6	*ingens*	13	Lower Cretaceous.
7	*Jenneyana*	10 or 11	Lower Cretaceous.
8	*Paynei* (?)	.....	Lower Cretaceous.
9	*Reichenbachiana*	16	Lower Cretaceous.
10	*superba*	.....	Lower Cretaceous.
11	sp. (Y. T. 434)	.....	Lower Cretaceous.
12	sp. (Y. T. 115)	13	Lower Cretaceous.
13	*excelsa* (?)	13	Lower Cretaceous.
14	*Marshiana*	9, 11, 13	Lower Cretaceous.
15	*colossalis*	10	Lower Cretaceous.
16	*Williamsonia tuberculata*	15	Oölite.
17	*mexicana*	10	Liassic.
18	*setosa*	18±	Oölite.
19	*spectabilis*	13	Oölite.
20	*whitbyensis*	14	Oölite.
21	*Weltrichia mirabilis*	12 (?)	Rhaetic.
22	*Williamsoniella*	.....	Oölite.
23	*Cycadocephalus Sewardi*	17 or 18	Rhaetic.

In closing the present résumé of floral characters in Williamsonian types, the great extent of sex diversity found fixes our attention because of the immense variation it not only theoretically permits, but actually indicates through very long periods of time. The uniform diœcism of existing cycads might be conceived of as long persistent or not; but not so the bisporangiate strobilus, which must have been a potentially bisexual axis far back toward the time when the ancestral forms attained heterospory. And this floral form, as was insisted upon when the first descriptions were given, must in itself be exactly the one capable of giving rise to the most varied phases of monœcism and diœcism. Just as *Cycadeoidea* is the key to *Williamsonia,* so the study of the showy flowers of the latter genus schools us in the collection and laboratory study of less conspicuous casts and imprints. These exhibit most unexpected structural detail, and constitute an immense new category of evidence of Mesozoic gymnosperm development of fundamental interest in any adequate theory of angiosperm origins.

Ascendancy.	Periods.	Persistence and relationship of great groups.
VII. Reign of Angiosperms.	Quaternary. Tertiary. Cretaceous. Comanchian.	
VI. Reign of Proangiosperms.	Jurassic. Triassic. Permian.	
V. Reign of Acrogens. (Higher Equisetes, Lycopods, etc.)	Pennsylvanian. Mississippian.	
IV. Reign of Gymnosperms.	Devonian.	
III. Reign of early land plants.	Silurian. Ordovician.	5. Actual fossil land plant record begins. 4. Primofilices; early Equisetes. 3. Basal plant complex with variety of species.
II. Reign of Algæ.	Cambrian. Precambrian. (Proterozoic.)	2. Differentiation of dry land and aquatic plants. (Fossil Algæ abundant.)
I. Reign of primitive life (hypothetic).	Old Precambrian. (Archeozoic.)	(Fossil Algæ begin.) 1. Primitive protoplasm and unicellular life.

The facts brought out in Chapters XIII and XIV go far to indicate long persistence of plant types, with wide gaps in all fossil series. The possibility that initial forms of existing phyla can ever be recovered is negligible. The chance that any other than pseudo-ancestral plants may be found is always exceedingly small. The recent development of paleogeography and the construction of many maps showing the extent of the continental areas subjected to periods of alternant emergence and subsidence throughout geologic time, proves the plant record to be slenderer than once supposed. It is mainly an invertebrate record which indicates the approximate outlines of the older continental land masses, and the direct record of the early upland floras is wholly lost; but as dominant or persistent plants emerge from a recordless past and reach a wider and wider distribution, the land deposits also increase until at last there is an essential correspondence between the fossil and existent floras. The nature of extinction is less understood than is that of direct evolution.

Instead of connecting the plant phyla at some point anterior to the earliest known occurrence as in the conventional *paleontologic tree*, it is preferable to leave all lines discrete where derivation is not absolutely proven. In the above scheme spacing and lineation are intended to convey relationship and derivation throughout. Lines of descent always tend to gradually converge in the past; but this fact is not here neglected. The groups are to be considered as arranged in the order of both time and relationship as if on an unrolled cylinder projected from a hemisphere, toward the pole of which the phyletic lines converge. This arrangement is a flexible one. In particular it throws the Lycopodiales and Araucariales next to the Cordaitales, without obscuring the fact that the main known relationships of the latter are Coniferous and Filicalean.

CHAPTER XIII.

CYCADOPHYTAN DISTRIBUTION.

In discussing the distribution of cycad-leafed plants, the outstanding topics are: (1) the restricted range of the existing Cycadaceans coupled with their exceedingly pauciform fossil record; (2) the immensely varied distribution and structure of the extinct types. The ecology of the existing forms is a relatively narrow, even if little and insufficiently studied, subject; conversely, that of the fossil types is a subject as broad as the field of Mesozoic plant life. These two subjects are, however, connected by the exceedingly close parallel between Cycadacean and Cycadeoidean stem structure. It was maintained in Volume I that the Cycadeoideæ are essentially cycads; and all later study has tended to confirm this view. Not only is it found that the fructifications in *Bowenia* and *Macrozamia* are lateral and that these genera have the same monopodial habitus as *Cycadeoidea*, but there is no great hiatus in any of the vegetative structures. As Chamberlain states the case, "there is no more difference between the general and histological structure of the stems of *Macrozamia* and *Cycadeoidea* than may be found between different genera of Cycadales."

As further suggested, it is in fact probable that all that prevents us from closely uniting existing cycads with some one of the extinct groups is the fact that the more primitive forms of the latter are still unknown. This close vegetative relationship between the Cycadaceæ and the Cycadeoideæ, however, permits very definite inferences as to the distribution of the latter; they must have lived in essentially the same surroundings and climatic formations, except for the relatively primitive forest facies. It is therefore in order to call attention to a few of the main facts in the ecology of the existing cycads as affording some explanation for their scarcity in past time. Subsequently the much broader topic of the proportion and distribution of cycad-leafed plants in the Mesozoic will be taken up at some length. The very patent fact that the heavy-stemmed cycads are distinctly unusual or extraordinary vegetal types also has a bearing here, but may be more conveniently made the initial topic of the concluding chapter on cycad derivatives.

SCARCITY OF FOSSIL CYCADACEÆ.

Considering their wide tropic distribution, the existing cycads form an exceedingly sparse element among gymnospermous plants. They seldom, if ever, pass beyond the limits of the thermal tropics or snow limit of the Torrid Zone. But they come very close to this limit both north and south, alike in Florida, Sonora, and in southeast Australia and South Africa.

It would be most interesting to know the relative proportion of cycads in the several climatic zones, the rain, monsoon, savannah, and thorn forests and the tropical grasslands and deserts. Being large-seeded plants, in any case slow to spread, and much given to growth in rocky situations, the cycads, however, occur so sparsely as a rule that no general data have ever been brought together.

In Florida the extreme northerly occurrence of *Zamia* must be close to 28° 30′, in somewhat rocky soils about the edges of the great hammocks in the west center of the peninsula beyond Clermont (reported). The chief occurrences are much further south, in the more strictly subtropical belt about Miami. The *Zamia floridana* affects the open pine woods, firmly rooting itself in the soft lime rock of the region, in some abundance; the *Z. pumila* is a much more infrequent type of the hammocks.

FIG. 82.—Xerophyllous vegetation of doleritic hills near Queenstown, South Africa. In the foreground *Aloe ferox* with *Encephalartos Friederici-Guilielmi*, and more towards the background scattered clumps of *Acacia horrida*. April. Photo by H. H. W. Pearson.

A close scanning of this highly interesting desert landscape shows the Acacias abundantly scattered about, and after them the Aloes. The *Encephalartos* seems to distinctly require the partial protection of the rocky ravines. The species of *Encephalartos* occupy similar dry, rocky situations as far north as the Uganda Protectorate (Lado, 4 N. L., 30 E. L.). Compare Fig. 96.

Mexico is no doubt one of the cycad centers of the world; perhaps it is not exceeded in any respect by Australia, much less by South Africa. There is not only much specific variety, but the *Dioon spinulosum* reaches a height of 16 meters in the Tierra Blanca region of Oaxaca, thus ranking with *Cycas media* as one of the vegetal wonders of the world. As in the case of the *Zamia floridana*, these tall cycads are found in some abundance, growing well-shaded among the prevailing limestone rocks. Chamberlain, to whom we owe their so very recent discovery, 1908, says:

"From Tuxtepec, a town on the Papaloapam River about forty miles southwest of Tierra Blanca, half a day's ride on horseback brings one to the mountains where *D. spinulosum* is as abundant as at Tierra Blanca. In some places it is the only large plant, and it would not be an exaggeration to speak of a *Dioon* forest."

There is perhaps no region in the world with a sharper or more varied differentiation of climatic zones than is found about the great peak of Orizaba and to the south along the serrated edges of the dry desert Mexican upland. These tall *Dioons* belong to one of the most favored of all monsoon forest belts. Taking altitude and moisture into consideration, as well as the fact that the cycads seem to require a dry season, the Tierra Blanca region must be a peculiarly favorable one.

FIG. 83.—*Encephalartos Altensteinii.* East London, South Africa.

Branched specimens and trunks scattered about among talus vegetation on the Nahoon River (compare with the *E. Friederici Guilielmi*, figure 82). Photo by H. H. W. Pearson.

Far less conspicuous is the average of cycad occurrence in the immensely varied Mexican country; one may ride through the mountains for hundreds of miles without seeing a single plant. Thus the form shown in Figure 101, Volume I, which Chamberlain assigns to his new species *Dioon Purpusii*, is evidently a type of the deep valleys which cut back into the edges of the drier semi-desert interior. It is reported from the Tomellin Cañon well shaded by bushes and small trees; also "at various places between Santa Catarina and Tomellin, growing in dry, exposed situations, associated with cacti and *Beaucarnea*." Yet one may, often enough without success, search in the situations apparently favorable to Cycad growth.

On a horseback journey from the interior through the mountains of southern Oaxaca to the Pacific coast at Minizo, despite the most constant watch, the writer found exceedingly few cycads. The *Dioon edule* grows very locally and sparingly associated with giant cacti on the Rio San Mateo just below the lower end of the great gorge between the Indian villages of Tindu and Tepojilla, about 15 km. southerly from the Barranca Consuelo. The altitude is here about 1,500 meters, above which the Cycads do not pass. This occurrence is further noteworthy because of the deep, warm, dry valleys favoring the growth of the

associated giant cacti, which are among the tallest if not the very tallest found in Mexico, the unbranched columnar trunks rising to a height of quite 18 meters. In strong contrast scarcely a plant was found in the forests about the foot of the main Sierra Madre escarpment to the south of Itundugia; neither was a single plant found about the Cerro de la Campana, a prominent peak of the first front range where thrives at least one *Marattia* (*lævis?*) with globular trunk full 40 cm. in diameter. Similarly, no Cycads were observed in open valleys of the lowest of the front ranges facing the coast, where tree ferns reach a height of over 40 feet; only in rocky places at the inner edge of the narrow savannahs next the coast was any indication of variety of species found. To the north of Minizo three species of *Zamia* occur sparingly, all small and inconspicuous. This sparing distribution must largely continue all the way along the coast to the Sonoran desert.

FIG. 84.—*Encephalartos Altensteinii*. East London, South Africa.

Unbranched plant growing in low growth forest on Buffalo River. Evidently the present species is not so distinctly xerophyllous as the *E. Friederici Guilielmi;* but, as noted among the Zamias, closely related species are found to cling more or less exclusively to forests or else to more open woods, as may be observed in the case of the two Floridian types. Photo by H. H. W. Pearson.

In South Africa it appears that the type of occurrence found in Mexico is again characteristic. It is said that the Stangerias form thickets on the Natal border, although no notes on the occurrence of the species have recently come to hand. Text-figures 82 to 85, of typical African occurrences, show that the Cycads may closely hug the desert. Concerning the greater part of African Cycad vegetation but little is known. *Encephalartos* extends through a belt several thousand miles wide, the sparing occurrence in the Uganda Protectorate (figure 86) being of great interest because of the complete parallel with the branched Cycadeoideas of Minnekahta.

The Australian Cycad realm is probably better known than the African. The fact that *Macrozamia* forms considerable forest stretches in southeast Australia has long been known. Chamberlain says that at Avoca, near Sydney, *Macrozamia spiralis* forms such dense thickets that one can hardly crowd his way through. Near Brisbane, on Tambourine Mountain, occurs *Macrozamia Denisoni*, one of the most beautiful of all the Cycadaceæ,

FIG. 85.—*Encephalartos Friederici-Guilielmi.* Queenstown, South Africa. April. Photo by H. H. W. Pearson.

Old plant above, which has shed the pinnules of its old foliar crown, leaving the bare rachides. Below a similar staminate plant. The six staminate cones are lateral in position. The stem apex here remains in a vegetative condition and eventually grows up through the whorl of cones. This is the case in both sexes in *E. Altensteinii* and *E. Friederici Guilielmi.* The (long) current statement that the cones of living cycads are always terminal is therefore inexact.

with cones weighing 70 pounds. *Bowenia* sometimes forms a dense but easily penetrated undergrowth in the *Eucalyptus* bush at Maryvale and Byfield, on the Tropic of Capricorn; and 700 miles to the north is found the dense jungle of the Cairns district. Of this, Chamberlain says (62):

"The profusion of palms, tree ferns, and various vines and epiphytes was bewildering. Along the streams *Angiopteris*, a remarkable fern, small specimens of which are occasionally seen in greenhouses, reaches a tremendous size, with leaves nearly twenty feet long and stalks as large as a man's arm. At Herberton, near Cairns, a beautiful tree fern, *Dicksonia Youngii*, is so abundant that it forms almost impenetrable jungles. Besides, in open places, all three genera of cycads found in Australia may be secured within a single day's tramp."

FIG. 86.—*Zamia paucijuga* n. sp. ×0.83. Frond of a subterraneous stem about 8 cm. in diameter, from north of Minizo, on the Pacific coast, Oaxaca, Mexico.

The pinnules are of a papery thinness, also noted in *Bowenia spectabilis* (Vol. I, Fig. 50), and have not been found included in described forms, reference to a new species being arbitrarily made. Study of the illustration (made in transmitted light) shows a certain tendency to a netted venation.

The very general though capricious distribution of the Cycads within the limits of the thermal tropics has been sufficiently noted for present purposes, and would in itself seem to indicate a widely dispersed ancestry. But it is also clear that the Cycadaceæ seldom

grow in situations favoring fossilization in times of periodic submergence. Does this latter fact, then, afford the main explanation for the great scarcity of fossil remains definitely referable to the Cycadaceæ? It may, although it seems that the very narrow range in geologic time of the comparable heavy-stemmed Cycadeoids may go far to indicate that they extended little beyond the periods in which they are found, the present-day group being a later development. Certainly it is a striking fact that the *Williamsonias* are always the abundant forms, and that not once has a *Cycadeoidea* locality yielded an undoubted cycadacean. Is it not a possible explanation that as many Cycadaceæ are now existent as at any given time in the past? Should it not require most convincing testimony to entirely remove a certain suspicion that the hundred-odd existing species were not all derived from about six Triassic or Jurassic species as a sort of recrudescent evolution following early Mesozoic decline or change in the ancestral line? Forms obviously primitive are easy to single out. *Cycas* and *Stangeria* are clearly old, the typical Zamiaceans probably more modern. As the mixed distribution of leaf-base bundles also appears in the Cycadeoideæ, *Encephalartos* may be of some older derivation. The *Stangeria* type of leaf occurs in the Lias of both Mexico and India, although the application of chemical methods has not so far been applied to the study of such leaves which are called *Stangerites*. *Bowenia* is, plainly, old and in size, habitus, and branching features comes astonishingly close to Cycadeoideans. In fact, it may well be that all the existing Cycad species are derived from one species each of *Cycas*, *Bowenia*, *Stangeria*, *Dion*, *Microcycas*, and *Encephalartos*, with perhaps two old species for the remaining Zamiaceous forms.

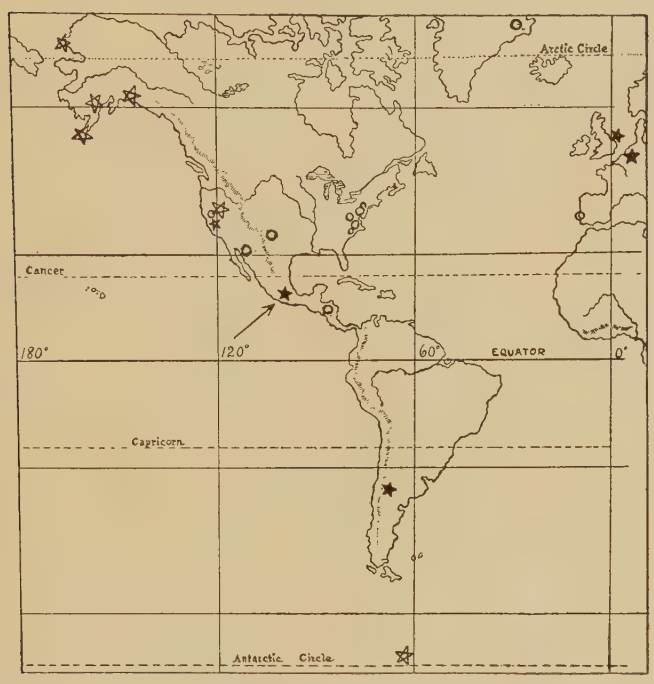


FIG. 87.—Principal Triassic and Jurassic plant localities of Western Europe and the extra-arctic Americas.

Circles denote *later* Trias; solid black stars *early* and outline stars *later* Jura. The arrow points out the newly discovered Mixteca Alta horizons of Mexico, where 600 meters of Liassic strata have been measured and true Triassic plants are also believed to occur. These plant beds are widely extended over the region stretching westwardly from the valley of the Nochixtlan River in Oaxaca to Tlapa in the State of Guerrero (or farther), and northwardly into southern Puebla. They are successional to the Honduran and Sonoran Trias.

Restated, there is, over and above the exigencies of fossilization, reason from the structural side to suspect that the chance for encountering post-Triassic Cycadaceans must always be slight. And, furthermore, a searching study of ecologic factors may eventually go far to lend color to the idea that, as just suggested, the existing Cycads are, in addition to being isolated, even a small recrudescent group descended from as few as 10 species, or one or two more than the existent number of genera. The Cycads are *par excellence* xerophylls, and doubtless a great rôle in the origin of new species has always been played by rain-forest and desert areas. The vast post-Mesozoic changes in the distribution of these areas must have constituted a factor of great magnitude in setting boundaries to the present distribution of Cycads. Since the rain-forests now contain, or at least tend to contain, fewer species than more arid regions, it is likely (for instance, in the case of *Zamia*,

the most prolific genus) that the transition to drier and drier conditions on the Pacific-coast side of Mexico has resulted in the evolution of some new species. One readily gains the impression that, taking the Cycad vegetation of Mexico and Central America as a whole, ecologic changes which have occurred in these areas in the near geologic past have been responsible for a certain amount of comparatively recent specific variation. The conditions now ruling in the south continental Cycad belts are of course those favorable to the Cycads, and they have obviously been of short duration. But whether or not the relative scarcity of cycadophytans in post-Cretaceous time is primarily due to an actual paucity of forms, it is, so far as one can judge from collections, unlikely that many Tertiary terranes containing notable Cycad florules essentially differing from those already known remain to be discovered.

THE CYCADEOID ELEMENT IN MESOZOIC FLORAS.

The Permian Cycadeoid line is meagerly known. The Cycadeoids first become dominant seed plants in the Lunz of Austria (Keuper), and so continue to the close of the Wealden. They thus typify the Jurassic, about equally overlapping the beginning close of that period. In the Rhætic the Cycadeoids first reach notable proportions; they culminate in numbers in the lowermost Lias of Oaxaca and begin to decline in the Wealden, few being left in the Upper Cretaceous. Cycadeoids occupy the interval between the disappearance of the Cycadofilicaleans and the spread of the Angiosperms; while coincidently with their decline, the conifers reach their greatest proportions in the recovered fossil floras.

Physical evidence of the *age of Cycads* is left behind in various florules and by no means inconsiderable beds of coal. Throughout, generalized tropical conditions prevail, and there is a world-wide uniformity in both the composition of the floræ and the trends of change observable in them. One of the most important of the Cycad coal series is that of the Tonkin Rhætic which now produces from 250,000 to 300,000 tons annually (*cf.* Zeiller, 425). The longest-known of the Cycad coal fields is of course that of Brora, so interestingly described by Hugh Miller (Popular Geology, p. 253) in a passage too long to quote, too interesting to abridge. According to Woodward, the Brora field is Bathonian, belongs to the great Oölite, and may be an equivalent of the Corn Brash (284). The Triassic coal fields of Virginia and North Carolina have been fairly productive and are a Lunz or a Rhætic equivalent.

The most recently examined field is that of Oaxaca, which in many respects recalls the Brora field, although distinctly older, being of lowermost Liassic age. The Oaxacan, like various other Jurassic coals, is a semi-anthracite, usually occurring in thin seams varying from a few centimeters to a meter or more in thickness, with a high ash content. In some of the leaner seams the Cycads are very abundant, and in all they make up a large proportion of the coal itself.

In scanning the older cycad flora components as closely as may be feasible, it is wholly unnecessary to attempt to separate Cycadaceans; they are for all practical purposes negligible, being merely the isolated analogue of the silicified series. The presumption is strong that the forms of unknown affinity are in all cases more nearly related to the Cycadeoids, always the dominant type. One of the most interesting of the earlier floras is that of the Lunz beds of Austria, although yet lacking a final description. According to Krasser (133) the Lunz flora of some 41 determined species consists of 44 per cent ferns, 39 per cent Cycadophytans, 2 per cent Conifers, 5 per cent Cordaitaleans, and 10 per cent Equisetums and Calamariales. The pre-Jurassic type of this flora is quite apparent when the large *Equisetum* element is

noted, and it is sufficiently emphasized that the rather high percentage of Cycadophytans is due to the fact that the Pterophyllums culminate in the Lunz and thus form in that period the crest of the first wave of the Cycadophytan advance in the Mesozoic, which reaches its climax in the Lias.

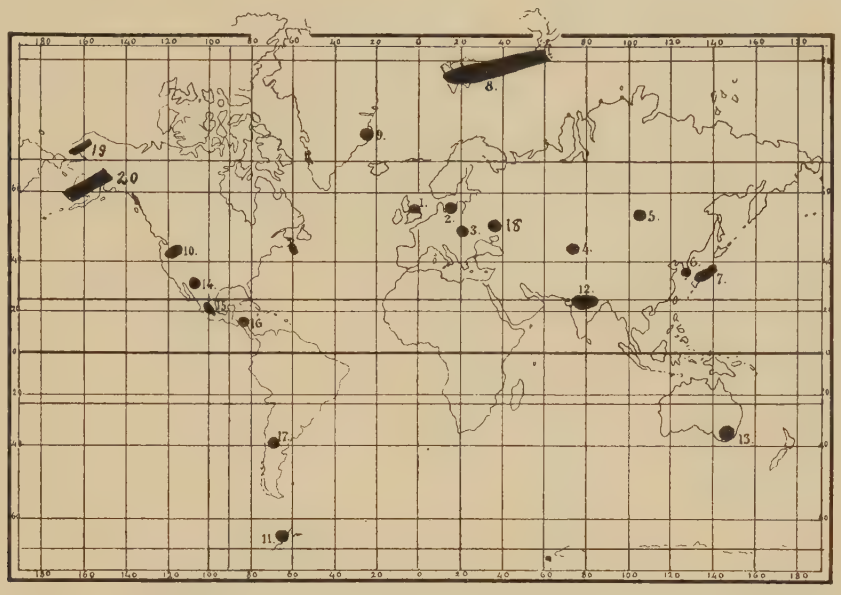


FIG. 88.—Distribution of principal Rhæt-Liassic regions yielding Williamsonian foliage and fructifications.

Various scattered Liassic and other mid-Mesozoic areas in Europe, America, Madagascar, and elsewhere are not indicated, though some of these, as, for instance, the Liassic of upper Italy (Zigno) and the Oölite of Sardinia (Krasser), etc., yield important fossil floras. This map shows the notable chain of localities on the Pacific coast of the Americas with the newly discovered Oaxacan region in the same latitude as, and on the exact opposite side of the globe from, its nearest analogue, in the Rajmahal Hills and Gondwanas of India. No. 17 represents fossil plant regions on both sides of the Andes.

In the Rhætic of Tonkin, which has been so admirably studied by Zeiller (426), the following proportions are present:

Classification.	No. of species.	Per cent.
Ferns (mainly older types)	26	48
Cycads (largely Pterophyllums)	18	33.5
Conifers (Ex. *Nœggerathiopsis=Cordaites*)	5	9
Equisetums	3	5.5
Ginkgo	1	2
Total	54	

These are almost identically the proportions observable in the Richmond-North Carolina coal fields, from which about 70 species of plants have been reported. Of these, ferns compose 49 per cent, Cycads 32 per cent, Conifers (and Ginkgos) 11 per cent, Equisetaleans, 8 per cent.

Necessarily the age of the various succeeding Jurassic floras can not always be accurately determined. There are many elements of doubt; the occurrences are far separated; they represent both northern and southern realms; while behind them lie hidden extensive

migrations. Not only so, but it is probable that adequate collecting has been done at very few of the localities; nevertheless, it is instructive to bring together the proportions of plants from several of the greater localities denoted in the accompanying sketch maps (Figures 87–89), as follows:

Classification.	Ferns.	Cycadeans.	Conifers.	Ginkgos.	Cordaites.	Equisetums.	No. of species.
Graham Land Mid-Jura	42	28	27	..	..	2	61
Sutherlandshire Great Oölite	36	25	24	9	..	3	86
Oroville Oölite	46	38	12	4	..	?	..
Oregon Jura (Douglass County)	33	40	17	8	..	2	..
Yorkshire Inferior Oölite	36	38	9	12	?	4	63+
Bornholm Lias	35	33+	17	9	?	5	76+
Rajmahal Hills Lias	32	34+	8	?	?	2	..
Oaxaca Lias to Rhætic	18	70	(2)	..	8	2	60+
Tonkin Rhætic	48	33	9	2	2	5.5	54
Average, per cent	37	39	14	4+	2+	3	..

In the foregoing table one of the most striking facts observable is the large proportion of Cycadophytans in the Oaxacan Lias. This is partly due to the fact that collecting has not progressed far enough to bring to light as representative a list of ferns as in the case of other sections; but it is equally certain that the list of Cycad frond species, and even genera, will yet be added to. That the Cycads will, however, continue to form over half the recovered flora is probable. Moreover, the Cycads are slightly more numerous in the lower division of the El Consuelo section, the detailed account of which should be referred to (394). Evidently the Cycadophytans culminate both in number and variety in the lowermost Lias. As the following table shows, the Cretaceous representation is markedly smaller.

Classification.	Ferns.	Cycadeans.	Conifers.	Angiosperms.	No. of species.
Neocomian, Japan	43	47	7	....	28
Upper Knoxville	38	38	11	(?)	36
Wealden, England	37	35	11	....	70
Wealden, Uitenhage	38	33	28	....	21
Kootenai	40	21	28	....	88
Wealden, Germany	54	18	21	....	33
Lower Cretaceous, Portugal	47	10	21	....	95
Potomac	32	25	22	17	134
Urgonian, Austria-Hungary	17	38	17	0	29
Komé	45	12	20	10+	75
Aptian, Portugal	28	8	44	12 (?)	23
Albian, Portugal	30	9	18	32	66
Average, per cent	40	23	22	14+	...

Summarily put: In the Rhætic flora half of the plants are ferns or "Pteridosperms," one-third are Cycads, one-tenth are modern gymnospermous types; while the dwindling but still distinct *Equisetum* element forms a twentieth part, and *Cordaites* still persists. In the Liassic only a strong third of the plants are ferns, mostly of modern type; while the Cycads increase from 40 to 50 per cent of all plants, and Equisetums and Cordaites tend to disappear with the advent of modern coniferous types. Obviously, as already inferred, the later

Rhætic and early Lias witnessed some of the most profound changes known in the history of plants. In the Rhætic, then, diversity of Pterophyllums with the complete recession of the Equisetums and Cordaitaleans are the dominant features. But the old types of ferns, presumably including many seed-bearing kinds, still continue to outnumber all other groups, and the displacement of the Cordaitaleans only seems to foreshadow the advent of the conifers, as yet far from abundant or well marked.

FIG. 89.—Map showing the geographical distribution of Wealden floras and a few slightly younger or older floras. From Seward.

(1) Northwest Alaska.
(2) Queen Charlotte Islands.
(3) Kootenai and Montana.
(4) Shasta group in California.
(5) Black Hills region uppermost Jurassic to Lower Cretaceous.
(6) Maryland-Long Island to Martha's Vineyard.
(7) Texas.
(8) Mexico.
(9) Peru.
(10) Tierra del Fuego.
(11) West Greenland.
(12) Spitzbergen.
(13) King Charles Land.
(14) Franz Josef Land.
(15) Yorkshire-Sutherlandshire.
(16) N. W. German-Belgian-French Wealden.
(17) Russia.
(18) Portugal.
(19) Egypt.
(20) Cape Colony.
(21) New Siberian Islands.
(22, 23) Japan.
(24) Korea.
(25) New Zealand.

The course of change in the early to the mid-Mesozoic forest components is thrown into strong relief by the table at the foot of page 216, showing the composition of 12 Lower Cretaceous floras:

Naturally there are sharp limits to the accuracy of any compacted form in which the mid-Mesozoic plant record may be presented; and of course the defectiveness of this record is accentuated by the small size and aberrancy of several of the floras more or less arbitrarily included. Nevertheless, neither the exigencies of fossilization nor yet the varying personal equation involved in the determination of these fragmentary records can wholly obscure the larger outlines. Generally consistent and salient are the following features of Cretaceous vegetation:

(1) *Cordaites*, which still held a fast-lessening place in the early Jura, leaves behind only a few lingering hypothetical forms like *Eolirion*.

(2) The Equisetums left over in the Jura-Rhætic groups are now positively reduced to present-day scant numbers.

(3) The high frequency of ferns represents the culmination of the mid-Mesozoic fern recrudescence due to the spread of the more strictly modern types.

(4) The persistent presence of conifers in numbers, at first sharply increasing and then followed by decline in both the percentage and actual number of species recovered, is in striking contrast to the moderate numbers of the Lower Jura. It may, in fact, be definitely accepted that, taking the world over, a strong fifth of Lower Cretaceous vegetation was coniferous. This is the proportion in the English Wealden, in the Potomac, and apparently in all the horizons where collecting has been most thorough. The 44 per cent of the Portuguese Aptian and 7 per cent of the Japanese Neocomian balance each other as abnormal proportions unquestionably due to lack of fortune afield. In a word, just as the early Jura was a period of vast reaches of Williamsonians, so quite all the Lower Cretaceous was the time of dominant coniferous forests which receded with the advance of the Angiosperms.

(5) The cycadophytan and coniferous elements quite exactly balance each other, the time when these gymnospermous types are to reverse their Jurassic proportions and retreat to the southward being near at hand.

In brief and compact form the rise and decline of the Cycad element in the Mesozoic floras has now been outlined, not so much for the purposes of the stratigrapher as for those of the student of evolution. In a certain sense, moreover, the facts which are still obscure, still hidden behind the veil of the fossil record, are fully as important as the facts recovered when we come to discuss derivation. It must be observed that conclusions as to the age of beds and the proportions of plants found in them are based on an exceedingly meager record. It is very curious to find that flora after flora includes from 50 to 75 or 80 species. That these floras (barring very obvious inequalities of conservation or of collection) should maintain so strongly a given trend of change all over the world is little short of amazing. Nevertheless, there is an ever-present inference that these floras are one-sided, and that in each instance there must have been a vast inland, mountain, and sub-arctic series of related types which "left not a rack behind." Have we not been too prone to look on the recovered record as largely testifying to origins? Some of the changes must certainly be connected with geologic periodicity as affecting conservation, and it begins to appear probable that the recovered record shows more of the nature of migrations and extinctions than of origins, which are found to go back further and further in time.

CHAPTER XIV.

CYCAD DERIVATIVES.

The dominance of Cycadeoids in the Mesozoic is established, as the investigation of the silicified types is gradually extended to related casts and imprints. The stem and floral diversity exemplified is the outstanding feature of early Mesozoic plant life; while a certain analogy between seed coats and floral envelopes is discernible. The derivation of Cycadaceans from Marattioid types was discussed in Volume I, and to this subject it is not now necessary to return; the broad question in the foreground is whether the Angiosperms were evolved from the Cycadeoid complex rather than from Conifers or Gnetaleans, if not of ancient and separate origin.

To set forth certain limits to the evidence bearing on this central problem is the object of the following topics rather than any formal discussion. The abnormality of the Cycadeoidean stem must be emphasized lest scant attention be given the fact that so far as stem structures are concerned, it is as logical to search for Angiosperm ancestors among the Cycadeoids as amongst conifers. It is also well worth while to observe that to a certain extent stem features taken with the fossil leaf record of the Magnoliaceæ indicate this group to have a long and varied history. The hiatus between some of the early members of this alliance and the more generalized Cycadeoids can not have been wide.

Many and important are the contributions which have in recent years enriched the literature bearing on the origin and wider relationships of the conifers, but it is significant that investigators are not in entire accord in interpreting their results. It is therefore desirable to briefly epitomize the competent opinions of the investigators themselves as to which is the primitive coniferous stock, and what the probable relationships to the Angiosperms. Of even more interest are recent studies of Gnetaleans, which about equally suggest relationship to the Angiosperms on the one hand and the Cycadeoids on the other. Which group was closest to the dicotyl line in early Mesozoic time is difficult to adjudge in the entire absence of a Gnetalean fossil record. But all emphasis must not be laid on the lacunæ of the fossil record. The origin of the great groups is found to extend further and further back into the remote past; and nearly all attempts to determine the sequence of modern plants have been more or less vitiated by an implication that the paleontologic record is far completer than there is any final reason to believe possible.

CYCADEOIDEA AN UNUSUAL STEM TYPE.

It is difficult to define just what may be regarded as extraordinary types of vegetation or to say in many instances just why one type is more unusual than another. In the final sense one group of plants is no more peculiar or extraordinary than another. All are the resultant of environment which quickly determines size and must in the end influence structure decisively. The willows of Spitzbergen, a few inches in height, are as much an example of extraordinary vegetation as the gigantic lobelias of the Ruwenzori Chain. In some instances, moreover, peculiarity of type may be said to extend the habitat—in others, to set the sharpest limits of growth. Here, however, it is merely desired to point out the main reasons for regarding *Cycadeoidea* as an unusual stem type, in order more exactly to

fix attention on the primitive or essential stem features which formerly appeared in more normal development in related types, and at the same time to accentuate properly the scantiness of the Mesozoic plant record, which has thus far set such stern barriers before all attempts to even surmise the home of the early dicotyls.

There is no simpler mode of picturing the peculiarities of the Cycadeoid stem type than to invite casual attention to a few dicotyledonous and gymnospermous types which may fairly be regarded as similarly peculiar or isolated. The selections made are by no means taken at random and in each case serve to indicate some critically important point, although such larger comparison could be much extended.

FIG. 90.—Unusual stem types. *Borassus flabellifer* in foreground, *Cocos nucifera* in background. From Pulney-Andy.

Megaphylly in the monocotyls, quite as distinctly as in large-leafed cycads, precludes vegetative branching. But, on the contrary, the branching of flower stalks reaches its most extraordinary development in *Corypha*, the great monocarpic "umbrella palm" of Ceylon.

In thus calling attention to the aplastic characters or general features of *Cycadeoidea* it is desirable to note: (1) the general significance of branching in the palms viewed as a fixed columnar type derived directly from or at least secondarily to the dicotyl line; (2) the ultimately branched character of many dicotyls; (3) the long persistence and specialization of coniferous forest types, as exemplified by *Araucaria;* (4) extreme isolation of types odd of feature and old, as exemplified by *Welwitschia.*

PALMS A FIXED COLUMNAR TYPE.

Branching in the palms is rare, but at once affords a parallel and a contrast to branching in *Cycadeoidea*. In previous discussions of the large-stemmed cycads the far-reaching significance of branching has been continually insisted upon. The widespread occurrence of branching in the existing Cycads was until recent years largely overlooked and the branched character of many forms received adequate attention for the first time in the first volume of this publication. Previously, both Cycads and Cycadeoids were regarded as typically columnar forms. Also, the presence of lesser branches in the Isle of Portland trunks had been overlooked; nor was the full extent of branching in the Black Hills types at once realized. The simple fact is that any increase of pith, whether in the exogenous or endogenous stem, tends to suppress branching; the final stem-bulk may remain the same, but the plant takes on a compacted and specialized form and is often of rigidly megaphyllous habitus. According to this view, both the existing and extinct Cycads of robust type are specialized and relatively modern. At least no final reason appears for supposing that all the Cycads are descended from an ancient stock uniformly large in stem and leaf—certainly not if any inference may be drawn from palms.

FIG. 91.—Unusual stem types, as exemplified in the fairly primitive dicotyledonous order, Fagaceæ. *Castanea vesca* in late autumn (4 miles north of Branford, Connecticut).

An extreme trunk growth is reached by *Castanea sativa*, the Mount Etna "Castagno di cento cavalli" having reached a circumference of 190 feet about the year 1780. (Compare with *Adansonia* as figured by Schimper, ref. 249, p. 367.)

Far more than Cycads, palms are distinctly heavy-stemmed, habitually unbranched, columnar types; yet they have not lost their branched character entirely. The flower stalk may branch to an extraordinary degree, but any such branching is an acquired character. However, branching like that of the *Borassus* and *Cocos*, Figure 90, and of the Doum palm *Hyphæne* may be regarded as an indication that the power to put forth vegetative branches is merely suppressed; and nothing is more reasonable than to assume the former existence

of freely branched types in the ancestral lines which led into the palms. Those figured also serve admirably to exhibit the very simple scheme of branching in some of the Minnekahta Cycads, with the difference, of course, that the main axis is elongate. But the parallel becomes complete when *Cycas* is recalled, as shown in Volume I, Figure 13.

A derivation of monocotyls from dicotyls supports these ideas and it is of interest to state the case in the light of recent results. The origin of Monocotyledons from the Archichlamydeæ in comparatively recent geologic time now seems to be fairly well established. *Palmoxylon* stems are well described by Stevens; others have been found by the writer in the Pierre or No. 4 Upper Cretaceous of the Black Hills "rim," and such occur in somewhat earlier European formations; but the isolated data available are insufficient to fix the advent of the palms. Wherever characteristic stems of modern type are found in even small number in the Cretaceous, the fact should be accepted as nearly certain proof that the given type was already old or well established at the period of its first occurrence. In viewing the palms as relatively recent a pre-Jurassic origin should not be excluded.

FIG. 92.—Unusual stem types as further exemplified by the dicotyledonous order Cactaceæ. *Pachycereus grandis* Rose, as photographed in Guerrero by Waitz. Even more magnificent examples occur southwest of Jojutla and northerly from Iguala.

Structural study of the cotyledonary development is far more satisfactory. Coulter and Land have studied the transition from dicotyledony to monocotyledony (72*a*), finding that the cotyledonary strands and first-leaf strands organize the cotyledonary plate, which in turn gives rise to the root poles and later determines the character of the stem cylinder. The cotyledonary apparatus is always the same, arising in the same way and varying only in the details of its final expression. As Coulter later states the case (70*a*):

"The terminal cell of the proembryo forms a group of cells; the peripheral cells of this group develop the cotyledonary ring or sheath, on which two growing points appear. One of these growing points soon ceases to be active, and the whole zone develops in connection with the other growing point; but at the base of the growing cotyledon a notch is left by the checking of the other growing point. This notch is really the space between the two very unequal cotyledons, which surround the

real apex of the embryo. The apex of the embryo is at the bottom of the notch, and not at the tip of the large embryo. This apex soon begins to form leaves, and the so-called stem tip appears issuing from the bottom of the notch, in a relation apparently lateral only because the two cotyledons are so unequal. Furthermore, when the stem tip is examined, it is found not to be a stem tip, but a cluster of leaves whose rapid development has aborted one of the growing points on the cotyledonary zone. All this is very obvious in grasses, and is equally obvious in any massive proembryo, but it escaped the earlier observers of filamentous proembryos. The general conclusion is that monocotyledony is simply one expression of a process common to all cotyledony, gradually derived from dicotyledony, and involving no abrupt transfer of a lateral structure to a terminal origin."

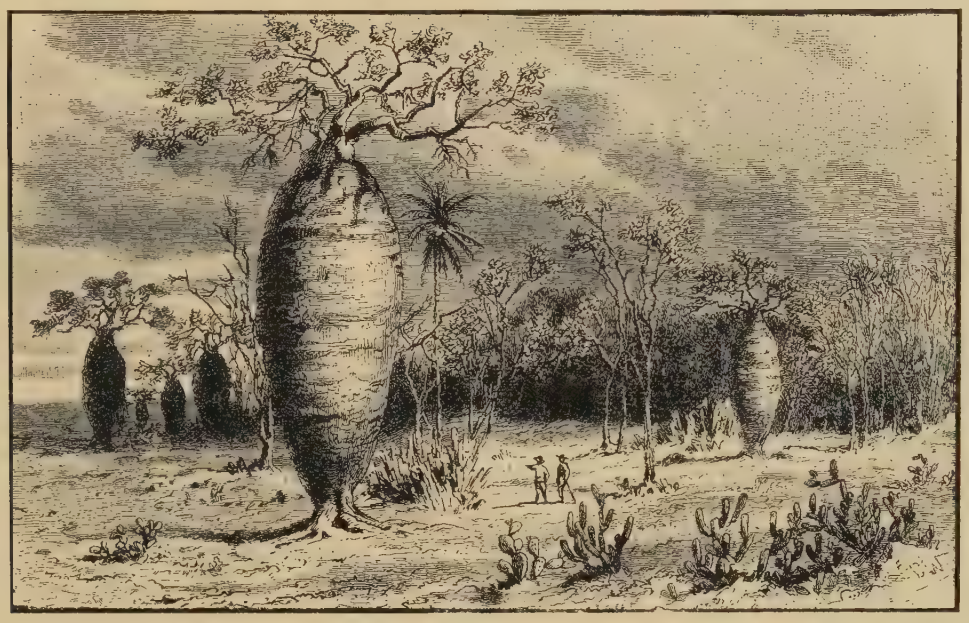


FIG. 93.—Unusual stem types—continued. Brazilian "caatinga" forest with the "barrigudo," *Cavanillesia arborea*, in the foreground.

Reaching a diameter of 5 meters, these singular relatives of *Adansonia* serve to still further accentuate the extraordinary stem diversity arising from climate and soil. Yet this plant may be placed in the same great group as an elm. From Kerner after Martius.

These interesting facts and the early appearance of dicotyledony in the Cycadeoids lend each to each a kind of mutual support. The inference is strong that typical dicotyledony in such a dominant group as the Cycadeoids must go far back beyond the origin of both dicotyls and monocotyls. The latter must then be relatively modern.

ULTIMATE BRANCHING IN DICOTYLS.

While it thus appears probable that in the monocotyls the branching habit is suppressed and finally all but lost, on the contrary it is in the dicotyls that extreme types of branching are developed, these certainly being coordinated with extensive secondary floral changes. In fact, it is unlikely that there ever occurred anywhere in the ancient plant world, or in pre-Mesozoic time, as freely branched a dicotyledonous tree type as the chestnut of Figure 91. There seems to be a sort of finality about such Ranalean types despite the rather simple if not primitive floral structure, and it is most difficult to conceive them as undergoing any change except in the direction of extreme reduction; and this conclusion is further emphasized by many and various types. In particular, the figure of *Adansonia* to be found in Schimper (249, p. 367) should be closely compared with the present text-

figure 91. Similarly, it is most difficult to see plasticity of either vegetative or reproductive structures in the earliest-known coniferous types; they are gigantic, ultimately branched on the excurrent instead of the deliquescent plan, and specialized. In particular the microphyllous character is so rigid that changes greater than those which find expression in new species, or at most genera, appear to be all but shut out, coniferous vegetation having culminated in the Lower Cretaceous. The inference is therefore clear enough that while in monocotyls the columnar habitus becomes fixed, exactly the opposite course of freer and freer branching leads towards finality of form in both dicotyls and conifers. It would seem that in both cases the ancestral plastic types go much further back in time than we as yet imagine possible and that they were neither large of form nor much branched.

FIG. 94.—Unusual stem types—continued. *Araucaria imbricata* growing in pure stands in the Andean foot hills of Neuquen, southwestern Argentina.

Notwithstanding the patches of snow, no more ancient-appearing landscapes than these can be found on the globe to-day. A very distinct likeness to *Cordaites*, strongest in the young forms, at once comes to mind. Photograph by Estéban C. Ferrari.

PERSISTENCE OF SPECIALIZED FOREST TYPES.

Fixity of type among branched forms is nowhere better exemplified than in the Araucarias, now quite as isolated as the cycads, and most conspicuous among gymnosperms for an exceedingly long and varied history, the later portions of which are fairly well known.

Araucarian forests, which no longer exist in North America, are a striking feature in Brazil and other parts of South America. Especially in Neuquen, a southwestern province of Argentina, in South Latitude 40°, there occur (well up in the front ranges of the Andes, where there is considerable snowfall) pure stands of *Araucaria imbricata*, which easily take rank among the most primitive of forest types. These have been in recent time cut off from the Araucarian forests of the Chilean side by the gradual rise of the Andean chain.

The trunks may reach 2 meters in diameter in favored situations, although small on the colder mountain sides. They rapidly shed all the lower branches and often rise straight as granite columns, with but slight diminution in thickness, to a height of 30 or even 40 meters, to support an umbrella-like crown of thick foliage. Such old trunks vaguely recall *Cordaites*, and the younger trees are for a long time no more branched than some of the Williamsonias. Indeed, forests more suggestive of a remote past or more ancient of aspect than these scarcely exist on the globe to-day. The landscape here shown finely illustrates the rapid decrease in size with increasing altitude or exposure and would seem to indicate that low warm and especially moist lands may have been the habitat preferred by the Araucarioxylons of past time; but a slow acclimatization is also exemplified (396).

This distribution is a net result of change since uppermost Cretaceous time and implies an actual southern retreat or restriction, like that of Cycadeoideans, beginning in the Cretaceous; for, although the recorded American fossil Araucariæ are for some unexplained reason few in number, characteristic types other than petrified trunks of *Araucarioxylon* do occur. The casts of the leaf-covered branches of *Araucaria Hatcheri* Wieland, a species very close to *Araucaria imbricata*, have been found lying on the skulls of Ceratopsid Dinosaurs in the Wyoming Laramie, a formation shown by Knowlton to be Eocene rather than Cretaceous; while a fine silicified strobilus from South Dakota bearing peculiar curved claviform seeds is called *Araucaria hespera* by Wieland and also pertains to the Laramie (388). In the typical North American Eocene the records are less well attested and cease entirely. The larger history of the Araucarians is further considered in succeeding paragraphs; the main point emphasized here is the extreme persistence of a vegetal type which has also continuously lent itself to frequent conservation in the fossil condition.

ISOLATED SPECIALIZED TYPES.

In extreme apposite position to the cosmopolitan and persistent *Araucarian* type stands "tumboa," ancient of aspect, wholly isolated, and now a form of singular and widening interest. The comparison of its staminate disk with that of *Cycadeoidea* (made in Volume I) was inescapable, and an even greater interest attaches to it, since the careful studies of the Gnetaleans by Lignier and Tison (160) which lead these authors to class the group among the Angiosperms. But the extraordinary leaf type of the "tumboa," if found as a fossil imprint, might never be recognized as having the slightest relationship to the leathery, pinnately reticulate veined leaves of *Gnetum gnemon*, which in no essential feature differ from dicotyl foliage.

Attention to the larger facts just cited and to any considerable series of unusual present-day plant types renders evident the necessity for relegating *Cycadeoidea* and the existing cycads to a lateral position in all theoretic lines of descent. Of far greater importance are the small-flowered, microphyllous, and plastic types of Cycadeoids, which must have existed in great numbers. *Wielandiella* (among these), with its slender bifurcate stems, reduced stamens, branches as small as those of many conifers, small leaves, and little-persistent leaf-bases is the type of unique importance so admirably studied by Nathorst.

In trying to picture the related and plastic ancestral type the highly specialized *Cycadeoidea* stems aid initially, but are no more characteristic of the greater outlines of Cycadeoid vegetation in the early Mesozoic than is a cactus or a "barrigudo" typical of present-day dicotyledonous vegetation. The Cactaceæ exhibit both a certain plasticity of stem type within very narrow limits and extreme isolation in the dicotyledonous series; the "barrigudo," a relative of *Adansonia*, is known as far back as early Eocene in France and shows an extreme stem specialization of somewhat similar character. A probably affinal Mexican

form (the giant "ceiba" or pyramidal *Bombax?*) which I observed in the Guerrero border north of Iguala, is quite as remarkable as the Brazilian "coatinga" type of Figure 93. The stem reaches a height of 30 to 40 feet, tapering evenly and rapidly from a diameter of 4 to 5 feet, the branches being reduced and sparse as compared with *Adansonia digitata,* and the leaves of small irregular form. But the point is that extreme types have doubtless existed in all ages and as seen to-day they emphasize beyond mere words the capricious character of the fossil record and the necessity for recognizing the fact that the very existence of such a specialized and aplastic form as *Cycadeoidea* implies, even without the Jurassic leaf record, the simultaneous existence of unknown series of related forms generalized in both habitus and structure. As Dr. Scott justly observes (262):

"At the present time, of all the vascular plants, that is, all plants above the rank of mosses, the Cycads scarcely amount to one in a thousand. In Jurassic and Wealden days, one in every three was a Cycad. If Cycads existed now in the same proportion to the whole flora as in Mesozoic times, there would be between 30,000 and 40,000 species of them, instead of the poor 100 or so which represent the class to-day."

FIG. 95.—Unusual stem types—continued. *Welwitschia mirabilis,* or Tumboa, growing in the Kalahari desert as sketched by its discoverer, Dr. Welwitsch. From Kerner.

One of the most exaggerated leaf and trunk forms known, Tumboa, as a plant type on the dividing line between gymnosperms and angiosperms, places an uncommon emphasis on the fact that in considering possibilities of relationship with Cycadeoids of bizarre stem type, attention must not be too much confined to specialized features.

From the study of the lowermost Liassic flora of Mexico and a careful comparison of Jurassic floras it appears that Dr. Scott's estimate of one cycad to every three plants in the fragmentary floras recovered is low rather than high. A proportion of 2 to 5 is probably nearer the truth and in the Oaxacan flora the Cycads thus far preponderate. Inasmuch as there is not the slightest reason to suppose that the total of all plant species was in the Mesozoic notably less than now, it is a safe inference that with the advent of Jurassic time the Cycadeoids numbered tens of thousands of species and exhibited a variety of stem and floral structure of which present forms, even when taken in conjunction with the Cycadeoideas, can give us but an imperfect conception.

Judging from the known and inferred development of Cycadeoid vegetation in Jurassic time, it is therefore clear that *Cycadeoidea* is wholly anomalous. But, notwithstanding the fact that the stem record is quite as abbreviated as the floral record, it is in a large measure distinctive. The structures already demonstrated, taken in conjunction with the long leaf record, render it necessary to regard the normal Cycadeoid as small and freely branched, microphyllous and small-flowered. The stems had a small pith, a thin cortex, and a fairly solid wood, with wood parenchyma and the power to develop growth rings. Such features are all known to occur singly or grouped, and it may be regarded as certain that far more generalized and plastic types than those already known must yet be found.

FIG. 96.—Unusual stem types—continued. *Encephalartos* growing in rock cleft near Lado, on the Uganda border, latitude 4 N., longitude 30 E. Photograph by Grabham.

The main stem, about 40 cm. in diameter, bears two huge ovulate cones and two (?) branches. Divested of its cones, such a plant of strictly tropic, dry and wet season, or desert environment, serves admirably as a restoration of a branched *Cycadeoidea* approaching maturity. The stem type is as bizarre as any of the foregoing, and it is only specialized features that separate it from *Araucaria*. The representative Cycadeoid types are those with heavy secondary wood, small pith, thin cortex, and little persistent foliar bases in alternating scale and leaf nodes.

Obviously enough, the presence of a thick cortical parenchyma in *Cycadeoidea* prevents any fair understanding of the leaf-trace and type in forms with a fully reduced cortex. Owing to the long course through the cortex, a very primitive bundle type is retained in which a "foliar gap" is formed as the single vascular strand of horse-shoe outline in transverse section leaves the main woody cylinder or siphonostele. The arrangement is essentially as simple as in the solenostelic *Loxsoma* (*cf.* Bower 32, Fig. 321); but the fact that it is from the upper and free edges of the leaf gap that branches and peduncle traces finally take their origin is less anomalous than at first appears, because with the wilting down of the leaf bases the cortical traces remain as so many projections of the woody cylinder. In a form with a very thin cortex, the leaf types would differ very greatly and the axillar

growths could play a far more varied rôle. Furthermore, because of the power to develop short nodes of leaves with long scale-leaf-covered internodes, it would be but a short step to the production of twigs bearing several nodes of foliage leaves succeeded by continued growth of the shoot with sparse leaves. In fact, features little removed from those of dicotyls are here reached, only stipulary growths remaining unaccounted for. However, a stipulary hypothesis is tentatively mentioned elsewhere in discussing the parallel afforded by the wood structure of *Drimys* and *Trochodendron*. Finally, the presence of wood parenchyma in some of the stems not only parallels existent Cycads, but indicates that the lesser stems had the power to become fleshy and plastic. The actual capacity for modification is most imperfectly indicated by the conservative types which make up the great bulk of early Jurassic plant facies.

PRIMITIVE MAGNOLIAS.

The simplicity of habitus characterizing magnolias of the present day can escape no one who takes the trouble to examine the young plants of the various species. In some of the younger plants the pith is relatively as large as in cycads and the stems have a bifurcate branch habit quite as simple as that of *Wielandiella;* while the long leaf-blades are not utterly unlike *Pterophyllum* fronds, and the great size of the distinctly *Cycadolepis*-like stipular leaf and flower-bud scales are striking features. Equally reminiscent of primitive types are the long-persistent leaf and stipular scars, and (above all), in the more macrophyllous forms, the alternation of short and long nodes of scars sharply recalls typical *Williamsonia* stem types; while the burst of huge amphisporangiate flowers is paralleled among gymnosperms only in the Cycadeoids.

The fact that stems referable to magnoliaceous types are not recognized in collections has no significance, and such might readily be mistaken for those of small Cycadophytes which are occasionally found. Thus Möller and Halle recently figured a Cycadophyte stem with scars in nodes, and much smaller than many of the magnolia twigs (179, Pl. 5, Fig. 11). But such a stem might just as well pertain to some early magnolia as to a low-growing or bushy Cycadophyte.

One of the most puzzling features of the dicotyledonous leaf is the stipulary outgrowth from the very point of insertion. This has always been most difficult to reconcile with any readily discernible feature of gymnosperm leaves, and it even seems necessary to go back and search among the *Aphlebia* outgrowths of Paleozoic fern fronds for anything suggesting the remotest parallel; but the suspicion may be ventured that there is some relation (as yet hidden) between scale leaves, *Cycadolepis* scales, buds-scales, and stipules. The fact that exactly in *Magnolia* the stipulary scale leaf greatly exceeds in size the leaf itself in the earlier stages of growth, and performs an enveloping and protecting function, may be wholly significant. May there not be some connection with the fact that in the Cycadeoids adventitious or axillary fronds present every stage of development from lesser foliage fronds down to ordinary scale leaves? The tendency for some kind of axillary growth, whether foliar or floral, to appear in all axils, may be another factor in point. It is, then, not inconceivable that in the course of time some Williamsonian came to develop in the axillary position two lateral bundle strands comparable to the normal pair of strands in *Cycas*, as the supply of a scale leaf which gradually came to take on a stipular form and function. This is only a speculation made in passing, which perhaps botanists may already be in a position to overthrow; but it would be most interesting to find Williamsonians of small-stemmed habit with the stem apex and its *Cycadolepis* scales and young fronds conserved.

It is positive that the Jurassic ancestors of the magnolias did not live within the zone of frequent conservation, and identifiable twigs of such are not likely to be found. Such

small branches are among the rarest of fossils. They simply lack the bulk which gives persistence in the fossil form and cling to the parent stems too tenaciously to drift into positions favoring fossilization. On the contrary, the leaves of early magnoliaceous species are very abundant and there is every reason to believe that the magnoliaceous type developed into a great Cretaceous complex including in particular *Liriodendropsis*. How abundantly the leaves and even imperfectly conserved fruits of magnoliaceous type have occurred in the past appears in Hollick's account of the Cretaceous flora of southern New York and New England (115).

The primitive magnolias are, therefore, not hypothetical; they were a reality; they existed, and in the vastest numbers spread all over the globe in early Cretaceous times. Not only so, but they must have had countless relatives of primitive type far more closely related to Cycadeous plants than any of the few magnoliaceous species or other Ranales now existent. Moreover, in the Ranales the primitive character of the flower is indicated not only by "apocarpy and hypogyny, but also by the strong tendency to the indefinite repetition and spiral arrangement of the floral members," and "were it not for the prevalence of a distinct calyx and corolla the alliance would not hold so high a rank." But it has been shown in the chapter on seeds that there is the strongest reason to suspect some kind of universal homology between seed coats and floral envelopes, and both calyx and corolla may just as well as not have been old structures, even in Jurassic time.

Furthermore, there is nothing in stem structures anywhere justifying the former supposition that magnoliaceous stems are remote from those of either cycads or conifers. It has already been shown that conceptions of Cycadaceous stems must not be based on extraordinary types and that on last analysis there is no broad line of demarcation from other gymnospermous types. Cycadaceous stems and coniferous stems are all interrelated and go back to Paleozoic time. Professor Seward says, too, that stems of the magnoliaceous genus *Drimys* are as simple as those of conifers. True enough, as Professor Jeffrey has pointed out to me, the lack of vessels may be modern and the apparently old features acquired. But the burden of proof rests on any such interpretation and the simple character of the wood in an allied form, *Trochodendron*, is very impressive. Dr. Bailey has with much kindness called my attention to this genus and at the same time has sent thin sections of the wood. The pitting of the spring tracheids is scalariform on the radial walls, resembling remarkably the scalariform tracheids of the Cycadeoids, while the summer tracheids have simple bordered pits. There are no true vessels and the alternating bands of spring and summer wood resemble those of a hard pine.

As Dr. Bailey says, the types of pitting, Araucarian, Abietineous, scalariform, etc., are so variable and dependent upon purely physiological factors that they can not be used without great caution for phylogenetic purposes; but the scalariform type of pitting appears again and again in the Araucarineæ, and older groups, as well as in the Angiosperms; it is highly characteristic in the Cycadeoids, which at the same time retain the Araucarineous pitting and have quite the most generalized wood and stem type among known gymnosperms. At one time the supposed lack of growth rings afforded a sharp distinction, but this hiatus has been effectively bridged and no especial importance can be attached to it in establishing any larger phylogenetic lines. In short, we have reached a point where it becomes necessary to find among conifers floral structures more nearly resembling those of Angiosperms than any yet discovered, before a conifer-Angiosperm line of descent can be accepted as anywhere near so probable as a Cycad-Angiosperm relationship. But let the facts be viewed still more closely.

CONIFER-ANGIOSPERM RELATIONSHIPS.

A fair average of botanical opinion on the position of the Coniferales in the *paleontologic tree* has been to the effect that the Cycadofilicalean derivatives of the Filicales gave origin to a Bennettitalean line, from which the Cycadales led off, and a Cordaitalean line from which first the Ginkgoales and later the Coniferales led off to at last give rise to Gnetaleans and Angiosperms. Latterly some of the ablest botanists have not only doubted the earlier view, but even discarded it altogether for the alternative of a Bennettito-Cycadalean Angiosperm ancestry. There are, however, well-defended variations from the two main trends of opinion; thus Lignier and Tison have finally come to assert that *Welwitschia* is actually an Angiosperm, although retaining a great number of ancestral gymnosperm characters (160). In this they are further sustained by still more recent study of Gnetaleans, both structural and embryological, carried out by Pearson and by Thompson (336, and later papers). Nevertheless it is probable that if a consensus of opinion could be had it would be found that a considerable number of botanists, if not even a majority, hold more or less tentatively to the old view of Conifers occupying the linear and primitive position.

The broad question of Conifer-Angiosperm relationship is slowly approaching an answer, a fact best brought out by a brief recital of some of the outstanding results of gymnosperm study during the past 10 years. *Araucaria*, Conifers, the Ginkgoales, the Gnetales, and *Cordaites* here come into consideration.

IS ARAUCARIA OLD?

Seward and Ford, in their study of recent and extinct Araucarians (293), regard *Araucaria* and *Agathis* as survivals from a remote past, forming with various extinct types a subdivision of the Gymnosperms, the Araucariales, which are held to have a Lycopodiaceous rather than a Cordaitean ancestry. In thus returning to an older view it is held that *Cheirostrobus* serves in some measure to bridge over the gap between the male sporophylls of the Araucariæ and those of Lycopodiales; that *Lepidocarpon* (which, as Scott says, must be included in the category of seeds) is a true link between the Araucarian seed and the normal Lycopodiaceous sporangium; that the Lycopodiaceous wood, with its scalariform pitting, is not sharply separated from the Araucarineous wood, normally consisting in tracheids with multiseriate bordered pits on the radial walls; that, as Penhallow (218) and others note, transitions between the pitted and scalariform sculpturing of the radial walls of the tracheids occur in various plants, recent and extinct; that the radially elongated elements with spiral and more or less reticulate pitting, which largely make up the medullary rays of Paleozoic Lycopods, have been lost by the Araucarians as a possible result of diminution in the primary xylem rendering superfluous any radial conducting elements of tracheal form. All of the points of comparison brought out by thus turning attention to the Lycopods can not be fairly given in brief compass, but various other authors stoutly oppose some of the contentions cited.

Jeffrey, throughout a series of papers adding greatly to our knowledge of the Mesozoic conifers (121–124), becomes the chief protagonist of an Abietineous derivation of the Coniferales. He holds that the leaves of the Cretaceous *Prepinus* are characterized by fibrovascular bundles identical in general organization with those of certain Cordaitaleans, true centripetal wood being present; he also finds in the Kreischerville deposits that at least seven distinct species of *Pinus* accompany this remarkably interesting genus *Prepinus*. According to Jeffrey:

"The Araucarineæ represent the abundant crown of the coniferous genealogical tree in Mesozoic time; but by their almost complete extinction in the important changes which ushered in the Tertiary period, a lower, more ancient, and overshadowed branch, the Abietineæ, became a new 'leader' and in its subsequent development very much obscured the original plan of phylogenetic development."

Thomson, in his important and thorough study of the comparative anatomy and affinities of the Araucarineæ (339), returns to the orthodox view of derivation from the Cordaitalean alliance, emphasizing these important points:

"(1) Leaf gaps are present in the stem and ancestral presence is indicated by occurrence in cone and seedling; (2) in leaf morphology, habit, and structure the Araucarineæ resemble Cordaitean forms, the double and multiple traces in the secondary wood finding a parallel in no other group of the coniferales; (3) Ray pitting of the tracheids in contrast to the specialized condition of the pine alliance is primitive, that of the cones even recalling the more primitive Cordaiteans; (4) resin tracheids, like those of the pines, occur in the root and cone axis of Araucarineans which, taken as the basal forms, indicate how the resin tissue in the modern conifers has been derived; (5) the medullary rays are without typical ray tracheids and consist of thin-walled unpitted parenchyma, though bent-ended tracheids associated with the rays may be the precursors of the ray tracheids, since such are found in Cordaitean forms and in the cone axis of the pines; the ray cells are thus practically identical with those of the Cordaiteæ; (6) the rays of the bast have no albuminous cells and periderm is of late development, a fact doubtless associated with the persistent leaf-base; (7) the Araucarineæ exhibit a variable development of growth rings, combining characteristics of ancient and modern forms. Where variable, it is not certain that the rings are *annual* and they are in part 'inverse' or even root-like."

There is a further passage from Thomson's paper (p. 8) which should be quoted in full and which deserves to be recalled by every paleobotanist who chances to handle cycadeous or *Brachyphyllum* stems:

"Another feature in connection with the leaf of the Araucarians is the persistence of its base. This is much better developed in *Araucaria* than in *Agathis* and remains green for many years in some cases and, together with the leaf or the remains of it, forms a protective outer coat to the stem. The 'armour' of the Cycads consists of just such leaf-bases and disorganizing leaves, but has alternating with them a series of scale leaves."

Thibout, in his monograph on the male flowers of Gymnosperms (324), holds, moreover, that the sporophyll structure and arrangement of the vascular tissue in the Araucariæ more resembles that of Cycads than in the case of any other conifers.

Owing to the further fact, therefore, that in the Araucarineæ leaf-gaps are present, as in the Cycad cylinder, the outer and morphological resemblances between the Cycadeoid and especially the early Mesozoic Araucarineous young branches and shoots have an inescapable significance. Also, if Thomson is correct in his statement that the principal Abietineous features which find a parallel in Araucarineous types occur exactly in primitive tissue zones, the advocates of a great linear extension of the Abietineous stock now occupy a more or less defensive position. On this point the two succeeding contributions indirectly bear.

Thomson and Allin (340) show that the claim for the great geological age of the Abietineæ based on the Permian and Carboniferous forms "*Pityoxylon Chasense*" and *P. Conwentzianum* is contestable. In the former, absence of annual rings, 1- or 2-seriate medullary rays with thin-walled unpitted parenchyma, and multiseriate alternate and hexagonal radial pitting of the tracheids indicate Cordaitean affinity, the wood being solid and without "resin canals."

Elkins and Wieland, in their study of the Cordaitean wood of the Indiana black shale (80), reach a general conclusion as follows:

"*Callixylon Oweni* is an advanced structural type which can stand in an ancestral relationship to other gymnosperms, or even be regarded as standing near to cycadaceous types, and slightly in advance of the actual line leading into the modern Araucarians. Moreover, this wood suggests that it may well be that both Jeffrey and Thomson are virtually correct when the one assigns a high antiquity to Araucarian, and the other equal great age to Abietineous, structures. The fact that the latter have undergone much variation in Cretaceous time, playing the great rôle in the Cretaceous coniferous forests, merely makes the ancestral Abietineous features harder to discern; whereas in the Araucarians primitive structures stand out in bold relief. At least it is evident that great variety of structure exists in Devonian woods, and considering the further diversity of the ancient seed types it begins to appear that if there is any past period which can be fairly singled out as the true age of gymnosperms it must be Devonian time."

It may be added that further evidence is being received in support of these newer views of ancient and polygenetic origins. Scott and Jeffrey have published a paper of especial interest to American paleobotanists, at last adequately illustrating the structure of the plant series from the base of the Waverly shale of Kentucky (266). The types are all ancient and in harmony with the assigned position at the base of the Lower Carboniferous, but being then well established could have a greater antiquity.

As just noted the tendency has been to trace the conifers back through the Cordaitales to the ferns. In so doing the Cordaitales are regarded more as a plexus than as a restricted group limited to the discovered forms. The discovery of the Cycadofilicales has gone far toward bridging the gap between the ferns and *Cordaites*. Professor Seward's separation of the Araucariales sharply challenges this current monophyletic view of conifer derivation, and it appears that there is a strong tendency to turn to the polyphyletic view.

Tison (242) would include *Saxe Gothea* and the Podocarps as terminal members of the Araucariales; also Robertson (236) would put *Phyllocladus* between the Podocarps and Taxoids, but nearer the former, though, according to Robertson (238), "the female flower of *Taxus* more closely recalls that of *Cordaites* than that of any other known plant."

However, Thomson, who so stoutly opposes Jeffrey's contention that the Araucarineæ are Abietinean derivatives and holds to the older view of Cordaitean ancestry, also suggests a broad division of the conifers (338). He emphasizes the opinion of Coulter and Chamberlain that the scale and its ovules in Abieteæ represent a highly modified axillary shoot corresponding to the spur shoot of the group, and believes the statement must apply as well to the Taxodiæ and Cupresseæ. He concludes as follows:

"There are, then, two great groups of the conifers * * * the simple scale group (Taxaceæ and Araucariæ), and the complex-scale series (Abieteæ, Taxodiæ, and Cupresseæ). Both forms have the ovules on the physiologically upper surface, a position rendered almost imperative by the necessities of the seed habit. This position, however, has been attained in two very different, but possibly equally difficult, ways in the aplo- and diplosporophyllous forms of the Coniferæ."

So far investigations of coniferous stem structure, nearly all the more important of which are cited in the bibliography, have not reached a degree of finality. It is generally agreed that the structure of the medullary rays is fairly characteristic, and considerable discussion has been given to the subject of ray tracheids. Jeffrey (124) finds traumatic ray tracheids in *Cunninghamia sinensis*. Miss Gordon (102) notes the presence of both marginal and interspersed ray tracheids in old stem wood of *Sequoia sempervirens*, but found in the fossil Sequoias no ray tracheids with a transition to parenchyma. Thompson (333)

regards the ray tracheids as cenogenetic because absent in older pines, *Pityoxyla*. But he considers that ray tracheids were present in the immediate ancestors of *Abies* (335), being now lost by reduction. Bailey recently placed the development of ray tracheids in the Upper Cretaceous (11); but Stopes (320*b*) finds these well developed in the Lower Cretaceous.

BISPORANGIATE CONIFERS.

There is much more possibility of a primitive bisporangiate condition in early coniferales than could possibly have been admitted previous to the discovery of the amphisporangiate flowers of *Cycadeoidea* as followed by the later determination that such flowers were of widespread occurrence throughout the Mesozoic. Nor, in any discussion of the older gymnosperm fruits, is it necessary to appeal solely to hypothetical bisporangiate forms of mid-geologic time certain to be discovered; much less to emphasize the fact that a staminate fructification, like that of *Cordaianthus Penjoni* strongly suggests termination in an ovuliferous apex. The bisporangiate flowers of Gnetaleans at once afford evidence that the monosporangiate character was less fixed in ancient times than later, and invite attention to the study of reverse strobilar growth in conifers. The conifers now have such specialized and highly modified sporophylls that no other line of attack can readily be followed in the absence of fossil evidence.

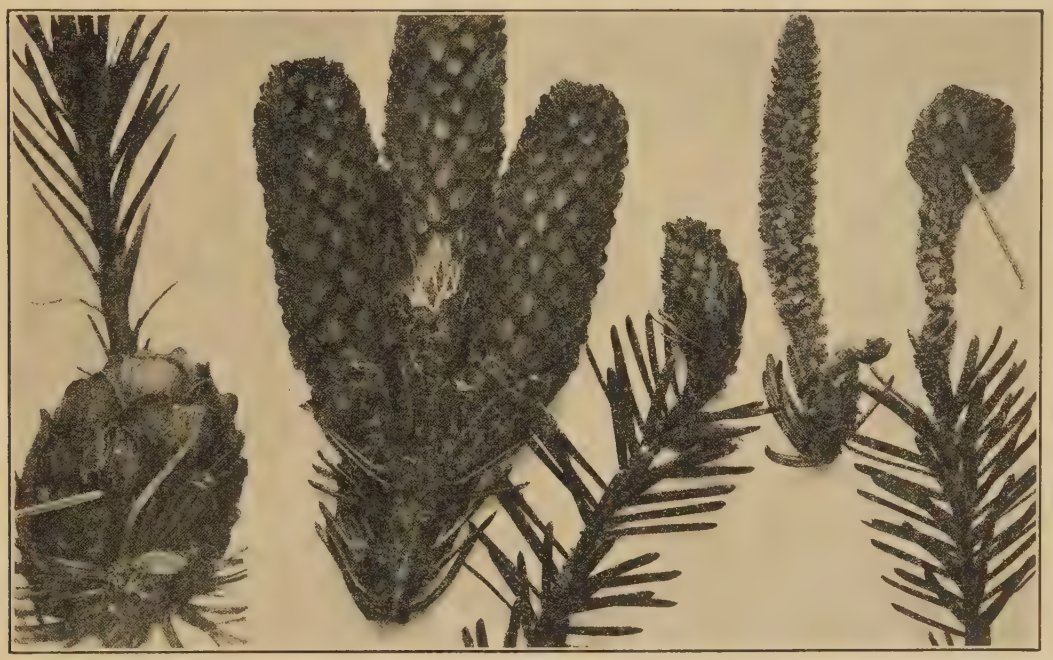


FIG. 97.—Reversive vegetative and sporangial growth in coniferous strobili. Axial extension of ovulate cone in *Larix* (to left). On the right, bisporangiate, normal staminate, modified ovulate, and both normal and modified ovulate strobili of Alcock's spruce (*Picea Alcockiana* graft on *P. bicolor*).

The study of abnormal coniferous axes has occupied the attention of many botanists, notably Čelakovský (53–56), and if not always conclusive is nevertheless highly suggestive. Figure 97 shows some recently observed examples which certainly suggest that conifers are not to be regarded as in any sense primitive types, that the reproductive axis of limited growth is in the highest degree modified, and that it is only because the megasporophylls have become so scaly, stony, and spiniferous if not senile, that the monosporangiate character has become so fixed. It is very interesting to see that in the Alcock's spruce the bisporangiate strobili proportionally increased towards the base of the small tree on which

they were borne, just as in many conifers ovulate fructification is mainly apical, and staminate fructification mainly basal. Younger Scotch pines and various other examples could also be cited; while even more striking than the bisporangiate strobili of any of the half dozen coniferous species thus far reported are those of *Pinus densiflora* (var. *Tanyosho*), which in some cultivated plants recur in abundance year after year. In this instance the amphisporangiate forms occur interspersed among the staminate groups and the resemblance to small flowers is obvious enough; the ovulate apex frequently grows forward after a basal production of pollen. A final study of the histology of such amphisporangiate growths has never been made; but observation of the axes through several years shows that they very closely approach the functionally bisporangiate condition, if not in some instances actually reaching it.

It would serve no especial purpose to cite results of embryological study of the conifers which may be considered to have a possible bearing on the origin of the angiosperms. More than mere argument, the general facts already cited serve to emphasize the truth that a derivation of angiosperms from the conifers does not especially rest on the results of more recent investigation. This idea rests mainly on hypothetic ground. It is as logical to derive angiosperms from the Cycadeoids on the basis of stem structure as from the conifers, and more logical from the floral point of view. If a larger generalization might be ventured at this point, it would be to the effect that the general results of the past 10 years have much weakened the theory of conifer-angiosperm derivation. It is true that the monstrous bisporangiate strobili may be regarded as partly reversionary. That there were ancient bisporangiate races which were closely related to the ancestral line leading into the modern conifers seems to be indicated; but the monosporangiate character of the conifers is a fixed character far back in time. The conifers must long since have passed beyond the point where they could possibly send off an angiosperm stock. If any of the angiosperms were actually derived from the conifers it must have been in pre-Triassic time. What the foliage of any such derivatives was like can only be conjectured.

The point which it has seemed desirable to emphasize is that it is not disproven that the conifers are polyphyletic; on the contrary it is certain that they consist in several races which are very old. Any possible derivation of dicotyls from this old line must go far back in time—very far beyond the Jurassic Sequoias and Pines, so like those of to-day.

THE GINKGOALES A PRIMITIVE RACE.

Next to the great question as to the relative age of the Araucarineous and Abietineous lines the position of *Ginkgo* has fruitfully occupied the attention of morphologists from time to time during the past 10 years.

Seward and Gowan, in their study of *Ginkgo biloba* (278), reach the conclusion that *Ginkgo* and the long fossil series forming the Ginkgoaceæ should not be included in the Coniferæ:

> "In many respects *Ginkgo* shows a marked affinity with the Cycads; like the extinct Cycadofilices, *Ginkgo* possesses Filicinean and Cycadean characters, but while exhibiting traces of the union of Cycads and Ferns, it represents in all probability a very ancient type which may have been merged into the Cordaitales in the Palæozoic era."

Tupper, in brief notes on *Ginkgo biloba* (346*a*), observes that in the roots, wood parenchyma and crystal cells are distributed in rows or series in radial planes, and that all the xylem parenchyma is radially distributed, not tangentially as in the conifers. It is concluded

that wood parenchyma, like annual rings, may be interpreted as a reaction to the arrival of winter conditions in geologic climate, and that the Ginkgoales are a "connecting link" between simpler and higher gymnosperms.

Lyon thus summarizes the essential features of the embryogeny of *Ginkgo* (163):

"(1) By free-cell-formation, following free-nuclear-division, a spherical protocorm is organized which completely fills the venter of the archegonium; (2) the basal cells of the protocorm, through combined activity, pass over into the blastema or metacormal bud; (3) the meristems of the stem and root are localized out of the one general meristem of the blastema; (4) cotyledons and leaves arise as exogenous outgrowths upon the growing-point of the stem and are here morphologically homologous structures; (5) cases are frequently met with, where two embryos from different oösperms have developed to maturity in the same seed; (6) polyembryony occurs, occasionally, through the production of two blastemata by one protocorm."

The outstanding fact is that in the organization of the dicotyledonous *Ginkgo* embryo the whole mass of compact tissue filling the oöspore is involved and in the absence of a suspensor the embryo invades the endosperm by direct growth. Embryologically speaking, *Ginkgo* is regarded as the least specialized gymnosperm. In a further paper Lyon (164) concludes that:

"The suspensor of a gymnosperm embryo is clearly not homologous to that of a lycopod or angiosperm embryo. In the gymnosperm the suspensor is developed between the body of the protocorm and the blastema and by its elongation serves to separate these two structures. In the lycopods and angiosperms, it is an outgrowth from the (more or less massive) protocorm and has one free end. In these embryos the metacormal axis is differentiated through the body of the protocorm."

Comparisons with *Araucaria* are not yet at hand; the first likeness is to *Cycadeoidea*.

In this connection it will be recalled that Coulter and Land, as noted at length on a preceding page, show the derivation of the monocotylar from the dicotylar embryo by suppression. Also Sargant (245) believes the primitive Angiosperms to have had two cotyledons which are likewise found in some Cycads, in all the known Cycadeoids, in the Gnetaceæ, in *Ginkgo*, the Cupressineæ, and Taxaceæ; while in *Agathis* there are two and in *Araucaria* two to four.

POSITION OF THE GNETALEANS.

Lignier and Tison (160) conclude, from their study of Gnetalean fructification, that *Welwitschia* is in reality an Angiosperm distinguished from all existent forms by the more or less complete retention of many ancestral gymnospermous characters. They hold that the mode of specialization in this lateral phylum has much resemblance to that seen in the Amentales. Whether or not the two lines occupy a linear position to each other, *Welwitschia* is regarded as essentially old and primitive and as affording (when compared with both other Angiosperms and the several gymnosperm groups) a fair *tout ensemble* of proangiospermous characters, as follows:

"Bois centrifuge formé de trachéides d'abord scalariformes (après les trachées), puis aréolées en spirale et dépourvu de vaisseaux; probablement encore du protoxylème centripète, mais peut-être seulement dans les feuilles; tissu de transfusion; plissements médulloséens de la couronne ligneuse avec tendance à l'isolement des faisceaux; canaux sécréteurs du type de ceux des Cycadales, des Bennettitales et des Ginkgoales; fibres hypodermiques; nervation dichotome.

"Rameaux reproducteurs simples, gros, à phyllotaxie spiralée, terminés chacun par une grosse fleur à phyllotaxie également spiralée dans toutes ses parties et couverts sur leur base d'appendices réduits à l'état de bractées. Fleur comprenant peut-être déjà un périanthe par spécialisation des bractées supérieures, un androcée sous-terminal et un gynécée terminal.

"Dans l'androcée, microsporophylles filicinéens isolés sur la spire génératrice, plus ou moins ramifiés, avec sporanges (ou peut-être, plutôt, synanges) abaxiaux ou latéraux et plus ou moins dressés; assise mécanique des sporanges épidermique, peut-être déjà partiellement réticulée; grains de pollen encore pluricellulaires, probablement même avec anthérozoïdes, en tous cas germant dans la chambre pollinique.

"Dans le gynécée, macrosporophylles très réduits, isolés sur la spire génératrice, déjà en cornet mais non encore fermés vers le haut (Hémiangiospermes), pluriovulés, les ovules y étant groupés sur la base du cornet, soit marginalement, soit à son intérieur; ovules tégumentés pourvus d'une chambre pollinique productrice d'une gouttelette collectrice micropylaire et d'un prothalle cycadéen; fécondation prédisséminatrice; proembryon; graines exalbuminées avec embryon dicotylédoné."

Full excerpts of recent researches on the Gnetaleans can not greatly aid in reaching ultimate conclusions as to the antiquity of the group. There is no need to cite the work of Hill and De Fraine on seedlings or of Pearson on the flowers of *Welwitschia;* while the descriptions of testal structure so like those of the Cycadeoideas have already been freely quoted from in the chapters on seeds. In general the study of ovulate structure and the presence of the staminate disk accentuate a Cycadeoid affinity; but on the contrary all larger comparisons of vegetative structures lead to more or less insistence on a coniferous derivation or rather analogy. Thus, Thompson concludes from his investigation of *Ephedra* (336):

"The idea of Cycadalean and Bennettitalean affinity receives little support from the anatomy of *Ephedra.* On the other hand, there are many points which are opposed to it, and in favour of Coniferous relationship; the arrangement of the primary vascular bundles, double leaf-trace, arrangement and structure of pits on the tracheides, bars of Sanio, tertiary spirals, trabeculæ and resin plates, primitive uniseriate lignified rays, wood parenchyma, and endarch vascular bundles of the leaf. The Gnetales do not appear to have arisen from any modern group of Conifers, but rather from or close to the base of the Coniferous line.

"An Angiospermous affinity is indicated by the possession of true vessels, broad rays, formation of broad rays by fusion, and separation of the leaf-traces on the stem."

It appears that the foregoing opinion loses slightly through a lapsus concerning the important feature of wood parenchyma which is present in both the Cycads and Cycadeoids. The latter are also carried near to the hypothetic Angiosperm line by the strong development of scalariform wood as noted in the section on primitive magnolias.

But still more recently within the past year Thompson (Amer. Jour. Bot. 2, No. 4) also finds angiosperm resemblances in the embryology of *Gnetum.* The pollen grains may germinate well up in the "style," the tubes growing down to the nucellus as in angiosperms. Male prothallial cells are not produced; only free nuclei form in the embryo-sac before the tubes enter, after organization of one or more eggs. Before fertilization the female gametophyte divides into numerous multinucleate compartments, in each of which all the nuclei then unite as a fusion nucleus. The endosperm is formed by divisions of the fusion nuclei in the lowermost compartments. It is suggested that the polar nuclei of angiosperms may be the complete analogues of the fusion nuclei of *Welwitschia* and *Gnetum.*

In extension, Pearson (Jour. Linn. Soc. Bot., vol. 43) finds that the primary endosperm of *Gnetum* is homologous to that of *Welwitschia.* This endosperm is, however, regarded as a new structure not found in other plants—the "trophophyte." Whether the endosperm of angiosperms is a highly modified form of such a pseudo-prothallus, as suggested, is a point which may yet bear consideration. Now that so many points of angiosperm contact have been found amongst Gnetaleans, it is necessary to insist that the presence of structures like the "trophophyte" may indicate antiquity as much as relationship. This is especially

true of the feature of bisexual spikes recorded by Pearson in *Gnetum gnemon*. These range from the strictly unisexual to the true bisexual form. Such a condition must not be taken as pointing directly toward contact with the angiosperms. Instead it signifies just as strongly a very ancient contact with the Cycadeoids. It may in short still be permissible to emphasize an earlier view of Seward (Ency. Brit., XII, 762*d*) that "it is not improbable that the three genera of this ancient phylum—the Gnetales—survive as types of a blindly ending branch of the Gymnosperms," which, albeit, "helps us to obtain a dim prospect of the lines along which the Angiosperms may have been evolved."

PERSISTENCE OF THE CORDAITEANS IN THE LIAS.

Lignier, in a description of various petrified woods of Normandy (150*a*), illustrates a stem from the Oxfordian, *Cormaraucarioxylon*, with a pith 2 cm. in diameter and numerous leaf-gaps, from which emerge the single persistent foliar traces of unusually fine conservation. The stem is thus of interest as occurring a little later than the last of the Cordaiteans, considered by Zeiller as still present in the Lias (421, p. 213) and found by Wieland (396) to extend into the time of the abundant Williamsonias of the lowermost Liassic of Mexico. Whether or not the Normandy specimens denote a last stand of *Cordaites*, as Lignier thinks not impossible, the size of pith raises the question whether a tendency to progressive medullar reduction is indicated. Such questions must remain long unanswered; but in a Cretaceous *Araucarioxylon* from New Zealand, described by Stopes (320*a*), which, like the Normandy specimen, has an extreme thickening of the rows of tracheids bordering the medullary rays on either side, the pith is small and the type a far later one, with strongly pitted ray cells and strong annual rings evidently seasonal. While, then, Araucarians go back to the early Triassic at least, *Cordaites* persists into the Lias and forms a little-known but impressive overlap of the more modern conifers.

CERTAIN GENERAL INFERENCES.

In every branch of paleontologic investigation the necessity for caution in the use of the recovered data continually increases. That the geologic record is a broken one is fully recognized by every investigator; how little chance there is that extinct species may be found in the fossil condition was descanted upon by Darwin. Yet with all the signs up, as data increase, often beyond all expectation, investigators are ever found in the same old rut, so easy is it to fall into the inadvertence of assuming a fullness of records which later prove meager in the extreme. It is only the proximate phase of this difficulty as met by the vertebrate paleontologist that J. W. Gidley thus aptly considers:

> "In the early attempts of vertebrate paleontologists to read the life-history of the globe as recorded by the fossil animal remains, it appears to have been too often assumed that the known fossils of a few widely scattered localities told the greater part of the whole story of the origin and development of the great groups of animals which have inhabited the earth, sufficient account not having been taken of the great number of chapters which are as yet unsupplied by the discoveries of collectors. Thus, in the genus *Phenacodus* from the Wasatch, Cope at one time believed he had discovered a generalized type from which had originated all the Perissodactyls. It is now known, however, that this great group probably had a very much earlier beginning, and it was not derived, at least, from any of the known condylarths. This is one of numerous instances in which too broad or sometimes obviously false generalizations have been made by investigators in their search among the incomplete fossil records for ancestral forms, and in their attempts at working out lines of descent. Even today a strong tendency toward this method of reasoning seems to prevail among paleontologists. It is usually assumed, in a general way, that the earliest-discovered recognizable representatives of a group indicate the actual first appearance of that group among the faunas of the earth,

and the absence of fossil remains of a group in the known collections is usually treated as indicating its non-existence. Such assumptions, while in great part excusable perhaps, have nevertheless resulted in the assigning of a much too recent date for the origin and differentiation of most, if not all, of the living orders and families of mammals, and doubtless have caused much of the confusion and disagreement that now exists among authorities in working out correlations and phyletic lines of descent. Many instances might be given in which recent discoveries have corrected errors of this kind, the tendency being to carry periods of origin further and further back in time. Thus, group after group when studied in the light of our increased knowledge is seen to have a much earlier beginning than was assigned it a few years ago."

The paleobotanist meets these limitations in full degree, and must even more continually turn back to an older and narrowing record of land life; the angiosperms reach well nigh their present development early in the Cretaceous without adumbrant forms; and now there has been added the even more startling fact that the disk-bearing gymnosperms, which the angiosperms seem to displace, were equally widespread and abrupt in their appearance at the beginning of Triassic time. But similarly the early seed types come wholly unannounced in the Devonian. Indeed, the suspicion grows stronger and stronger that disks, cupules, bracts, more or less sepaloid and petaloid structures, as well as more or less staminate organs, have existed in vast abundance from early Devonic time down to the appearance of the disk-bearing gymnosperms and the early angiosperms. Almost invariably, from the Devonian on, it has been mainly xerophyllous lacustrine or swamp types which form the great bulk of fossil plants. Even the 3,000 species of Carboniferous time afford only a one-sided picture of the specialized coal-swamp floras; no glimpse is had of contemporary mountain or upland florules.

As further brought out in Chapter XI, there appears to be a much greater separation of all existent types in time units than was once conceived possible. Nathorst found, in the upper Devonian of the Bear Island, Filicales, Sphenophyllales, Calamariales, and Lycopodiales (188) and he remarks: "One needs but to inspect briefly this florula of the Bear Island to see that vascular plants must have existed for an exceedingly long period previous to Upper Devonian time." The basis for a frontal advance was already established in Devonian time. Older conceptions of the categories of extinct types require revision; there is reason to suspect that existent groups of plants have come down as discrete lines from very remote time. This is probably the main reason why systematists find such great difficulty in reconciling the more typical existing groups in any classification expressing both relationship and descent in any other than the most general terms.

It is, however, readily seen how in the past schools have tended to arise, as the result of the uneven rate of discovery in different fields. Thus, the highly organized wood of the ancient Equisetes was earlier regarded by Brongniart as essentially phanerogamous. Long discussion between English and French paleobotanists followed. Had it been learned in the early part of the last century that *Lepidocarpon*, with its close approach to gymnospermous testal structure, was the fruit of *Lepidodendron*, the descent of all the gymnosperms from Equisetes and Lycopods would have been stubbornly contested. Professor Seward's view of the derivation of a separate Araucarian line is a partial return to these earlier views. If in one instance the one-sided character of ancient floras so often prevents recognition of phyla, in another, absence of fossil testimony should not be permitted to obscure relationships resting with some security on structural data.

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DESCRIPTION OF PLATES.

PLATE 1. *Cycadeoidea marylandica* Ward, ×0.465, and the U. S. National Museum type *Cycadeoidea mirabilis* Lesquereux, shown natural size (photographs 1, 2). The photographs 3 to 5 of *Cycadeoidea marylandica* show trunk fragments from the Iron Ore Beds of the Potomac formation of Maryland, presented to Professor O. C. Marsh by their discoverer, Philip T. Tyson, in 1867.

Photographs 1, 2.—Cycadeoidea mirabilis Lesquereux. ×1.

These photographs of the original and only type show (1) the polished transverse section and (2) the armor surface with leaf-base spirals undisturbed by fruit emergence. (See detailed description in text, page 109.)

Photographs 3 to 5.—Cycadeoidea marylandica. ×0.465.

Attentive study of the two Yale specimens illustrated in photographs 3 to 5 shows that they may belong to one and the same trunk. The range of leaf-base scar from distinctly rhombic to a characteristically scalene triangular form is clearly indicated. The small number of bracts about the basal portion of the peduncle which was elongate is also noteworthy. From four to six appear quite regularly in both specimens; although still more distal conservation would show presence of a few more bracts.

Photograph 3 is from a polished transverse section cut at a distance of about 1 cm. beneath the trunk surface shown in photograph 2. The large amount of ramentum and the elongated flattened section of the several peduncles are to be observed. Of these four are denoted by the numerals I to IV, which correspond in the two photographs. No bracts appear, the peduncles being in each instance cut beneath the insertion of the lowermost bracts.

Compare with the figure of *C. Fontaineana* in U. S. Geological Survey, Monograph XLVIII, Plate LXXXVI, which shows striking similarity. See also the photographs of the Link cycad (Plate XC) and Gray cycad (Plate CIV) which are referred by Professor Ward to *C. Bibbinsi*, but show similar peduncle and bract features accompanied by habitually rhombic leaf scars with wholly minor differences mainly dependent on ramentum conservation and weathering of the individual specimens. Nor do the large bract and leaf-base scars of characteristic specimens of *C. Bibbinsi* (*cf.* plate 2) in themselves prove the validity of this latter species.

In the text the fact is sufficiently emphasized that the Maryland Cycadeoideas are, so far as macroscopic characters go, essentially monotypic. But the fact that the fruits all appear to have projected beyond the armor is in itself no proof that but a single species is present. Such might be the condition throughout a family. The point is that *depth of conserved armor is as much a changing feature as length of peduncle in the entire group of silicified stems.* However, anyone may judge for himself how uniform is the presence of few and large bracts by taking up Monograph XLVIII of the U. S. Geological Survey and examining attentively Plates LXXXIII, figure 3; LXXXIV, figures 1, 3; LXXXVI, XC, XCI, XCII, XCIX, CI, CII, figure 2, and CIV. Even more striking does this series become on further noting that the type *C. Uhleri* (Plate C) also pertains to it, the bracts being merely small and young; while the type *C. Fisheræ* (Plate CV) has the same general habitus with bracts in a still younger stage of growth. This last-mentioned trunk, were it not for the somewhat peculiar appearance due to its accidentally drooped leaf bases, would unquestionably have the usual elliptical to conical trunk form and normal armor type of the *C. Uhleri* and other forms. This subject is further illustrated on the succeeding plate.

PLATE 2. *Cycadeoidea Bibbinsi* Ward. ×1. Specimen from the Iron Ore Beds of Maryland. Now in the collections of Goucher College, Baltimore. (No. 1484.)

This armor fragment is of especial interest because of its finely conserved surface, permitting very direct comparison with Black Hills trunks, several of which have much similarity, but not exact specific identity. The bracts surrounding the fruits are here far less numerous than in any of the Black Hawk specimens, and relatively few in number, as in most or all Maryland trunks and in *C. Uddeni.* Only peduncles come to the surface and the more or less projecting fruits uniformly fail of conservation.

The present fragment has never been adequately figured, though appearing in U. S. Geological Survey, Monograph XLVIII, Plate LXXXVII, figure II, 2 in miniature. It is known as the "Linthicum fragment." As explained more at length in the text, the Maryland cycads may include more than one species. If so, forms like the present would represent a second rather more columnar and distinctly larger species than the original *Cycadeoidea marylandica.* But the species *C. Bibbinsi* can at best be provisional, since one finds on going through the list of Maryland trunks a virtual specific identity in all cases where conservation permits a fairly close comparison. The present specimen is recorded on page 461 of U. S. Geological Survey Monograph XLVIII.

PLATE 3. Texas and Isle of Portland Cycadeoideas, illustrating small amount of change in outer form from Jurassic to Upper Cretaceous time.

Photographs 1 to 3.—Cycadeoidea Uddeni, sp. nov. Yale specimen No. 805. ×0.4. From the Upper Cretaceous ("Upson Clays") of Maverick County, Texas. Locality: 3 miles north by 0.5 mile west of Paloma. Horizon: "Upper" clay. (*Cf.* full description in text, page 113.)

1. Entire specimen mainly consisting in an armor slab from a moderately large trunk. Some of the wood is attached, the cortex being of medium thickness. To the left above a portion of the outer armor is sawn away.

2. Polished surface of a section cut through the outer armor, disclosing the scattered peduncles of fruits with several of the basal bracts attached in each instance.

3. Selected portion of armor disclosing to somewhat better advantage the form of the leaf-base scars.

Photographs 4, 5.—Cycadeoidea microphylla. From the "dirt bed" of the Portland quarries in the Isle of Portland. Three specimens were secured by the writer in 1907 through the courtesy of the officials of the Portland stone quarries for the cycad collections of Yale University. These include the fine trunk of photograph 4.

4. Specimen 803. ×0.3. The features of the original Buckland specimens with the smaller-sized leaf bases plainly recur. Observe in the bottom of the drill-hole from which was removed a core for sectioning the transverse sections recalling the features in the Buckland drawings. Note droop of thick ramental covering.

5. Specimen 801. ×0.35. In this specimen the ramentum has failed somewhat of the striking preservation noted in the preceding trunk. In both specimens there is much checking in the outer armor which obscures surface features, fully as characteristic as in any of the Dakota cycads. And to this checking is due mainly the difference in appearance between these trunks and those of the Black Hills and Maryland. The Portland trunks were more or less macerated before silicification set in. The Texas cycad *C. Uddeni* presents some of the outer armor checking and is distinctly intermediate in this respect. While there can be no doubt that the Texas specimen is specifically distinct from any of the Isle of Wight specimens, the presence of a new genus is not determinable. The peduncles of the Portland specimen are much the larger.

These Isle of Portland specimens are, despite their more or less macerated condition and checked exteriors, of the deepest interest, because they show not alone the form and habitus of the trunk but many structural details when adequately sectioned, besides occurring *in situ* in such great abundance. Consequently these photographs show not only an interesting variation in conservation, but trunk types which are second to no others in their general importance. Several of the specimens have been sawn through longitudinally, in particular the fine *C. microphylla* trunk, photograph 4. The woody cylinder is no heavier than in *C. dacotensis*, the pith nearly as large, the armor as thick, and the somewhat turbinate trunk form is due to less perfect silicification of the apical region. The apical suggestion of a polyxylic condition is found wholly deceptive. A few deeply embedded and very young fruits are present. (*Cf.* p. 92.)

PLATE 4. Representative group of 21 Black Hawk, South Dakota, Cycadeoideas, showing habitus and range of specific variations. ×0.09.

This group was selected as an exhibition series, including the principal species which occur at the Black Hawk locality. It also includes all the most important and striking of the types there found.

The species represented are the low-growing smaller forms, *Cycadeoidea rhombica, C. cicatricula, C. Stilwelli,* and *C. formosa,* and the great columnar trunks *C. Jenneyana* and *C. ingens,* as follows: *Cycadeoidea cicatricula,* No. 642; *C. rhombica,* No. 630; *C. Stilwelli,* No. 105; *C. formosa,* No. 89; *C. Jenneyana,* Nos. 91, 171, 101, 102, 113, and 551; *C. ingens,* Nos. 100, 103, 117, 178, 122, 592, 614; *C. ingens* (??), No. 115.

Casual examination of the above series shows a striking specific development within the limits of the columnar form. The trunks vary from the smallest to globular, and finally columnar stems of the largest size known among fossil cycads; the leaf bases vary from small or minute to full 5 cm. in width; the woody cylinders pass from thin types to the heaviest known; and the fruits likewise vary from small to large, including the largest known seed cones of the flatly convex parenchymatous cushion type.

Among these trunks occur forms with leaf-base bundles of both the patterned and diffuse type. Finally, the specimens illustrate general habitus effectively, despite the fact that the great *C. ingens* type is the only complete specimen. Taking this species first, No. 100, the type bears the fine crown of leaves which was the first discovered among the fossil cycads; No. 117 is a base showing the heavy form of the wood zone in transverse section, while No. 178 shows a basal segment of a trunk divested of both armor and cortex, and No. 614 a longitudinal section; No. 208 is the trunk bearing the fine leaves illustrated in the volume on structure.

Cycadeoidea Jenneyana is nearly as well illustrated by the two fine summits, Nos. 91 and 171, and the fine suprabasal segment 102 with a much thinner woody cylinder than *C. ingens.* The mid-region segments Nos. 101 and 551 indicate *C. Jenneyana* to be the tallest Black Hills species.

Trunk 115 is of rare interest. Both the large ovulate and staminate strobili are present, as described in the text.

The general habitus and fructification of the lesser species of the Piedmont-Black Hawk group is far less well known than in the larger forms.

PLATE 5. Woody cylinder types in Cycadeoidean trunks from the Piedmont-Black Hawk locality. × about $\frac{2}{5}$. In the four upper photographs the light or thin type of woody cylinder is seen in about the same development in two very different species. In the lower figures a third species is shown in both the basal and mid to upper transverse sections of a trunk with much of its armor broken away. (See text-figure 11 for view of armor.)

It is not believed that the trunk types of Figures 2 to 4 would ever show such heavy woody growth as the specimen of photographs 5 and 6. But it is at all times necessary to scan the dimensions of the medulla, woody cylinder, and cortex of such trunks with attention to the height at which the sections are cut. Owing partly to conservation, partly to the labor involved in cutting representative sections of the entire trunks, the requisite data for compiling a table of approximate woody cylinder dimensions for the several species are not at hand.

Photographs 1, 2.—Cycadeoidea Stilwelli, Yale specimen No. 105.

Photograph 1 shows the polished transverse section from the mid-region of the trunk. (*Cf.* Figure 2.)

Photograph 2.—The type, evidently a segment not passing beyond the mid-region of the trunk, since neither basal nor apical tapering begins.

The transverse section of figure 1 is distinctly oblique, the position being shown by the upper border, this view having been taken after the polishing was complete. The important point to note is that notwithstanding obliquity the thickness of the wood zone remains fairly constant.

Photographs 3, 4.—Cycadeoidea rhombica, Yale Cycad No. 630.

Photograph 3.—Transverse section showing even development of woody cylinder. As in preceding species, there is little indication of thin or incipient growth rings.

Photograph 4.—Lateral view of trunk segment. It is not known what the fruits of this form were like. It is doubtless closely related to the preceding. Both trunks evidently approach the full or fruiting size.

Photographs 5, 6.—Cycadeoidea ingens (*?*), Yale specimen No. 656.

Photograph 5.—Transverse section from very near base of trunk, showing nearly complete elimination of the medulla. Growth rings appear. The maximum development of the woody cylinder here seen may be partly due to the very low level of this section.

Photograph 6.—Transverse section of the same specimen as preceding photograph, cut about 20 cm. higher up and showing rapid diminution in thickness of the wood zone, but not the very thin type of quite unvarying thickness characterizing the two preceding species. The most of the armor of this specimen is broken away, although enough remains to show the leaf-base characters. Turn to the photograph of the lateral surface, text-figure 14.

PLATE 6. *Cycadeoidea Jenneyana* and *C. ingens* (*?*), n. sp. Specimens presenting typical variations in armor features, and showing how the degree of armor erosion may prevent exact specific assignment on the basis of outer characters alone.

Photograph 1.—Cycadeoidea (*McBridei*) *Jenneyana*, Yale Cycad No. 110. ×0.26.

Trunk showing variation in armor surface resulting from preservation of ramentum far enough out to pass beyond the more distinctly enlarged portion of the leaf bases of markedly subrhombic or lozenge-shaped transverse section.

The basal armor is broken away well down into the region of scant ramentum, while the upper armor is perfectly conserved and bears abundant ramentum as the leaf bases narrow into the free rachis. Here the form of the cavities left by the decay of the leaf bases or their failure to silicify varies but little from that of various other trunks of the present species; hence the heavy outer ramentum must very generally have been present when erosion of the trunks from the matrix began.

Photograph 2.—Cycadeoidea Jenneyana, Yale Cycad No. 115. ×0.26.

This Black Hawk specimen is of great interest because of its fruits. Two flowers situated within 15 cm. of each other were sectioned, the one proving to be bisporangiate with the elongate type of parenchymatous cushion (No. II); the other (No. I) being a well-advanced ovulate form with the strictly convex form of cushion.

The specimen is therefore the first definitely proven example of a truly monœcious trunk, for it is hardly probable that such a marked difference in the ovulate cones of like flowers would ever occur; as far as observed, cushion types, though varying much in the degree of elongation, are constant for the species.

The mid-segment of the trunk figured was found to surmount a basal segment, as appears in the group figure, plate 4. Other fruits than those indicated are present at various points in the armor, but are less distinct (see text description of these fruits, pages 40–42):

I. Ovulate strobilus with convex cushion. Sectioned. (See text-figure 11.)
II. Bisporangiate flower; microsporophylls 13, central ovulate cone with conical cushion. Sectioned.
III. Bisporangiate flower (?). Not sectioned.

Photograph 3.—Cycadeoidea Jenneyana. ×0.252. A fragmentary Black Hawk specimen, No. 554 of the Yale collections.

The general agreement in form with trunks 110 and 115 of photographs 1 and 2 is the result of unusually fine ramentum conservation, notwithstanding the nearly complete loss of the leaf-base ends. In this and the preceding specimen peculiarities in trunk features and conservation exactly recur, exhibiting a sharp contrast to the puzzling variations seen within one and the same species where more varied factors of preservation and erosion from the matrix had their effect.

Photograph 4.—Cycadeoidea sp., Yale specimen No. 642, from the Piedmont-Black Hawk locality. A trunk type somewhat variant from the foregoing, and adjudged a possible new species on the basis of structural features.

PLATE 7. Piedmont-Black Hawk Series, continued. *Cycadeoidea ingens* (photograph 2) and *C. Jenneyana* (photograph 1) contrasted. Both photographs are about one-third natural size.

These two basal trunk segments, numbered 102 and 117 in the Yale collection, are in nearly the same mature stage of growth. In the *C. ingens* trunk no fruits appear, in the *C. Jenneyana* trunk scattering young forms are present. The regular subrhombic sections of the large leaf bases in *C. ingens* contrast with the more triangular form in *C. Jenneyana*. In the latter, armor conservation usually extends farther out than in the *C. ingens* trunk; but this can not account for all the differences of form and also the marked variation in wood-zone development so apparent in the transverse sections of these fine bases given on the two succeeding plates. Trunk 102 is photographed on Plate 8, and trunk 117 on Plate 9.

PLATE 8. *Cycadeoidea Jenneyana.* Trunk from Black Hawk, now No. 102 of the Yale collections. Transverse section of lower or middle region of stem. ×0.355.

Although not so well conserved as the *C. ingens* trunk of the preceding plate, it is considered advisable to illustrate the present *C. Jenneyana* section in sufficient enlargement to facilitate comparison. For while this section must be from somewhat higher up on the trunk, this fact scarcely accounts for all the differences observable. The proportion between the cortex, armor, and medulla remain nearly the same in both trunks, but here the woody wedges have only one-third to one-quarter the development seen in *C. ingens* and are, consonantly with smaller and more numerous leaf bases, far more numerous. A very large medullar constriction dome is present.

PLATE 9. *Cycadeoidea ingens.* ×0.48. Transverse section through basal region of a large to full-grown trunk. Yale specimen No. 117, from the Piedmont-Black Hawk locality.

The section traverses the trunk just above the basal curvature, where the full diameter is reached at a height of about 30 cm. At *C* the cambium line of the wedges of the woody cylinder is especially clear, the xylem measuring 2.5 cm. and the phloem 1 cm. in thickness. The total thickness of 3.5 cm. at this height, however, diminishes somewhat on the opposite side of the trunk, which, owing to slight obliquity of the trunk section, represents a higher point. Correspondently the cortical parenchyma here increases slightly, but its average thickness is quite exactly 1 cm.

The emergence of the horseshoe bundles from the woody-cylinder gaps and their segmentation into subcircular pattern fully 1 cm. in diameter in the cortex may be very clearly observed.

The huge medulla, 13 cm. in short by 17 cm. in long diameter, is silicified in an unusual and striking manner. Evidently with increase in size the pith failed to occupy all the medullar space, leaving a dome-shaped constriction towards which the silicifying media infiltrated in curving lines which no doubt connect with the leaf-trace meshes of the woody cylinder. At the height of the section the dome-shaped pith constriction chances to be over 6 cm. in diameter and is a striking object, assuming the present explanation to be correct.

In résumé it may be noted that 35 collateral wedges go to form the woody cylinder, 2.5 to nearly 4 cm. thick, the xylem being about twice as thick on the average as the phloem, or markedly more towards the base of the trunk and showing numerous and distinct faint lines interpreted as weak growth lines. The thin cortex 1 cm. thick is followed by the armor of heavy leaf bases conserved to a distance of from 6 to 10 cm. out. The trunk being large but not old, bears no fruits, the armor being composed solely of leaf bases.

Unfortunately, no satisfactory complementary longitudinal section of a well-conserved *C. ingens* trunk is as yet available for purposes of illustration. The interesting basal fragment of a large trunk, Yale specimen No. 614, mentioned on page 80 of Volume I, where exact measurements are given, has been polished in the radial longitudinal plane and, although not yielding a sufficiently good photograph for reproduction, makes an excellent study specimen, showing very clearly how the xylem steadily decreases towards the apex in these forms; in the basal half meter of altitude from 8 to 4 cm. in thickness, the pith being fairly large. At the same time, the cortex must be relatively thickest at about two-thirds of the trunk height.

The most important specimen so far available for comparison with the present forms is Yale trunk No. 178, illustrated in Volume I, Plate XIV, photograph 1, as probably referable to *Cycadeoidea Jenneyana* (Vol. I, p. 78). This fine woody cylinder must, however, be either a *C. ingens* or an undescribed form. All that it has in common with *C. Jenneyana* is the markedly columnar outline, but the wood greatly exceeds that of *C. Jenneyana* and is distinctly heavier than that of any *C. ingens* trunk, except perchance the type in which the woody cylinder is not yet known.

PLATE 10. *Cycadeoidea Jenneyana.* Yale trunk No. 113. Polished tangential surface traversing the outer armor of a columnar segment from the upper middle region. Weight 45 kg. Photographed natural size. This polished surface is continuous with the further portion shown in the succeeding plate. Plates 9 and 10 should be further compared with Plate 12 and various text-figures.

The leaf bases of the specimens in both the present and the succeeding plate are cut well out from their insertion and for the greater part but a short distance beneath the outer surface of the armor. The section is thus exactly comparable to that of plate 12. Here a slightly younger stage is evident, only scattered bracts indicating the extreme summits of the bract husks of various incipient fruits. One or two larger fruits may be present, but such are not conserved.

The normal leaf-base section is here quite different from that seen in Plate 12 and very characteristic. It would seem from this feature alone that these trunks are specifically distinct. Furthermore, the dispersed bundle distribution is more in evidence. As in the specimen of Plate 12 there is great variation in the size of the leaf bases and even more probability that a considerable number of scale-leaf bases may be present. But, curiously enough, the lesser bases tend to conform to a general type, just as in Plate 12. In the present specimen, however, the leaf-base irregularity is so marked that notwithstanding the fact that the fruits are young, the leaf-base spirals are less evident than in the *Cycadeoidea ingens* specimen of Plate 12. Nevertheless, inspection shows that only the members of an uninterrupted spiral series are present. Consequently few or none of the lesser bases can represent adventitious leaves like those described in the case of Yale trunk 208, Volume I, page 94. See the view of the present specimen (No. 113) in the group of Piedmont-Black Hawk trunks, Plate 4.

PLATE 11. *Cycadeoidea Jenneyana.* Continuation of polished tangential surface of Plate 10, which compare.

The persistence towards the base of the trunk of the same characteristic features seen in the more apical part of this large section is striking. The smaller leaf bases are in about the same relative number throughout the entire 40 cm. of trunk altitude photographed; but near the base it seems that several adventitious leaves may be present, this point being difficult to decide. To the right the section passes out on to the armor surface, the rugose ends of several of the leaf bases not being polished off. At the lower left side a sort of banded and mottled agatization somewhat simulates the bract sections, for this reason partly obscure; but inspection reveals the presence of many bracts.

PLATE 12. *Cycadeoidea ingens* (*?*). Yale trunk No. 122, from the Piedmont-Black Hawk locality. Tangential section through armor of a segment from the mid-region of a columnar trunk of medium size, weighing 25 kg. Photographed in exactly natural size.

This is an instructive section passing from the armor surface at the upper left-hand corner of the plate to a depth of about 2 cm. near the middle of the plate and again emerging at the trunk surface on the lower right-hand corner. At the upper right-hand corner two peduncles with their lowermost bracts appear, this part of the section being a little more distal than the lower left-hand region, where a single peduncle is cut just below the level of the lowermost bract insertions.

The woody cylinders of 10 peduncles are so distinct that notation is not required. These peduncles indicate a young series of fruits. At the center of the plate the normal subtriangular section of the leaf bases is in evidence, the tendency to convexity of the upper surface being strong; but inspection of the entire plate shows every here and there lesser leaf bases varying in pattern and more or less fluted, in part no doubt because of the gradual wilting-down process and periderm excision to which the armor was at all times subject. However, the condition seen here indicates that the leaf bases must have normally varied very considerably in size; the presumption is that not infrequently there was a reduction to a strictly scale-leaf condition. These lesser leaves form a considerable group at the lower side of the plate, although the peduncles are observed to emerge in the usual axillary position. These ever-recurring variations in the size of the leaf bases of most columnar trunks make specific determination in the absence of positive knowledge of the woody cylinder and flowers nearly impossible in the case of almost the entire Piedmont-Black Hawk group, the extreme regularity of the leaf-base form in *Cycadeoidea Stilwelli* and *Cycadeoidea rhombica* being conspicuously excepted. Careful inspection of the plate reveals the aligned type of bundle pattern with some tendency towards a dispersed type. A partial passage from dispersion to alignment is in fact discernible. The splitting-up or fraying of the cortical traces with subsequent alignment is the simple explanation; and any such dispersion of bundles is in any case no more than a specific character.

PLATE 13. The *Cycadeoidea* collection of the State University of Iowa, at Iowa City, Iowa, made by Professor Thomas H. Macbride at the Minnekahta locality in the summer of 1893. Originally this collection included four additional handsome trunks which were sent as an unconditional present to William Carruthers, and are now deposited in the British Museum at South Kensington. This was the second collection to be made at Minnekahta, the first having reached the U. S. National Museum in the early spring of 1893. (See Vol. I, page 8.) $\times \frac{1}{12}$.

This magnificent assemblage of Cycadeoideas, representing as it were the pick of the greatest of all fossil cycad forests, tends for this very reason to contain only the trunks of the most striking of all the Minnekahta species, *Cycadeoidea dacotensis.* The original type is indicated by the arrow. To the right of it is the specimen Professor Ward denominated as distinct and called *Cycadeoidea McBridei.* There is evidence that it is not a *C. dacotensis*, and forms subsequently referred to *C. McBridei* (for example, Yale trunk No. 8) are of a different species. To the left of the arrow-marked specimen is a single fork from a large clump referable to *Cycadeoidea Marshiana.* One or at most two of the lesser fragments bear cones of the *Cycadeoidea Wielandi* type; but all the large and conspicuous trunks evidently illustrate the habitus of *Cycadeoidea dacotensis*, to which species they may be provisionally referred in bulk. From one of the larger trunks at the center of the plate was cut the bisporangiate axis illustrated on Plate XXXIV, Volume I, although I find myself unable to place the exact specimen in this view. The great majority of the fruits borne by all these trunks are young. (For enlarged view of *Cycadeoidea dacotensis* type see Figure 1.)

PLATE 14. *Cycadeoidea* (*colossalis*) *dacotensis.* ×0.35. A flattened subspherical member of an immense clump of trunks. Yale trunk No. 2 (weight 281 pounds).

From the appearance of the base of the present specimen it is quite certain that it grew close to or was still in organic contact with other and similar trunks or branches of huge size, forming a clump or branching specimen more or less similar to the forms shown on Plates VI to XIII of the volume on structure.

The trunk or branch is especially interesting for the fine conservation of the outer features of the armor. Several initial lesser branches and various scattered fruits are present, these all being small and young. Among the little projecting branches that to the left, surrounded by small leaf or scale-leaf scars, is of interest. It could in this instance be assumed that the trunk, although so large and robust, is still inclined to grow forward rather than enter upon a period of full fruition.

PLATE 15. *Cycadeoidea (colossalis) dacotensis.* ×0.35. Yale specimen No. 2 from Minnekahta, South Dakota. Apical view of the flattened, subspherical trunk. (See preceding plate.)

This cycad is one of the most interesting of the large specimens of branching habit, because it shows only slight lateral-branch development, although the mature size has been reached and growth of fruits has begun. It thus forms a connecting link between the columnar and branched forms.

Most striking is the parallel afforded with the great type *Cycadeoidea ingens*, shown in similar apical view in Volume I, Plate II, in the same degree of enlargement as the present specimen. Both trunks being of almost exactly the same size when viewed from above, direct reference to the figure of *C. ingens* should be made. The macrophyllous habitus of *C. ingens* is in strong contrast to the microphyllous type here illustrated.

PLATE 16. *Cycadeoidea (minnekahtensis) dacotensis.* Segment of the armor of a large trunk bearing numerous large but still young ovulate cones, the staminate disks having been shed just previous to fossilization. Yale specimen No. 24. ×0.4.

About a score of fruits and the more or less worn projection due to a well-advanced branch appear in this view. It will be noted that the fruits approach a regular quincunx arrangement, though because of their great size they occupy but a relatively small number of the leaf-base axils. The fruits appear to be, without exception, ovulate forms, some of which had grown to presumably half the mature size following disk dehiscence. (The arrows I–III show the position of three adjacent fruits illustrated on the succeeding plates.) This view forms the subject of Plate LXXVII, Nineteenth Annual Report, U. S. Geological Survey, Part II.

PLATE 17. *Cycadeoidea dacotensis.* A portion of the preceding armor segment containing the two fruits denoted by the arrows I, II, in the photograph; natural size.

Photograph 1.—View of armor surface showing fruit I to the left above, and fruit II to the right below. The two fruits are traversed by the longitudinal saw-cut which yielded section 959, photograph 1, Plate 19.

Photograph 2.—Transverse section parallel to the armor surface of the preceding photograph at a depth of about 3 cm., as indicated by the base-line of section 959, Plate 19. The peduncles of fruits I and II are cut just beneath the base of the cones they bear, the full bract series appearing with diagrammatic clearness. (*Cf.* enlarged view on the succeeding plate.)

PLATE 18. *Cycadeoidea dacotensis.* Photograph of a part of the section shown in the preceding plate (photograph 2), enlarged to three times the natural size.

Only at the present considerable enlargement do some of the lesser structural features begin to appear to the eye. In particular one notes the exceedingly small size of the ramental hairs which evidently formed a more or less silky mass. The peduncle cylinder with the bundle supplies of the uppermost bracts is outlined, though it may be that the regularly distributed excurrent bundles on the lower side of the figure are in reality disk-supply bundles. Observe that the base of section 959 is only separated from the plane of the present section by saw-cut distance, while the cone borne by this peduncle is shown in corresponding enlargement by photograph 2, Plate 19.

PLATE 19. *Cycadeoidea dacotensis.* Continuation of Plate 18.

Photograph 1.—Longitudinal section 959 (T. 24), natural size. This section was cut after the completion of the transverse basal section, photograph 2, Plate 17. The two ovulate cones being so accurately located in that section, the present section was next cut in a true median plane for both cones I and II. The arrows of Plate 18 also show the plane of this section.

Fruit I in this section is not further illustrated in this series of plates, but the nearby fruit numbered III in the photograph of the trunk segment, Plate 16, is in quite the same stage of growth and a little better conserved in the apical region. Photograph 1, Plate 20, shows fruit III in full longitudinal section, including the peduncle, while the accompanying photographs 2 and 3 bring into full view the characters of the young seeds.

Fruit II of section 959 is plainly in a younger stage of growth than fruit I, unless indeed the ovulate zone has aborted and a purely staminate condition is present, the matured disk having been shed. That a functional disk was earlier present is certain, some remnants still being present. (*Cf.* the enlarged view, photograph 2.)

Photograph 2.—Part of section 959, three times enlarged to more adequately illustrate the young seed-zone tissues, gum-canal systems of the cone axis, and other features. Through an oversight this enlarged view was photographed from the reverse side to that seen in photograph 1. The characters only begin to appear at this enlargement, which is the lowest sufficing to bring the bract ramentum into view. At the base of the photograph the disk shoulder is visible to the right and there is a strong suggestion of a dehiscence zone cutting transversely across the peduncle. If this were the only known specimen the features would no doubt be interpreted as indicating a monœcious habit.

PLATE 20.—Half-grown ovulate cone of *Cycadeoidea dacotensis;* also aborted (?) and mature ovulate cones of *C. Wielandi.* Continuation in part of Plate 19.

Photograph 1.—Cycadeoidea dacotensis. Longitudinal section of ovulate fruit III Yale trunk No. 24. For position on trunk see Plate 16, axis III. Natural size (section 916).

Owing to the fact that this section is cut in the radial and median vertical plane, the form and habitus are especially clear. The section extends down to insertion on the cortex and it is of interest to observe once more in these large

and striking fruits how the peduncle with its bracts, cortex, woody cylinder, and large medulla repeats the normal trunk form. Such a fruit is in itself a scale-leaf-covered branch ending in a strobilar crown. The details of the seed zone appear in the succeeding photographs 2–3.

Photograph 2.—Cycadeoidea dacotensis. Section 927, Yale trunk 24. ×3.5. Transverse section (tangential) through seed zone of the preceding axis. As this section passes close to the seed-stem insertion and includes about as large an area as can be cut from such a cone, it very fully reveals all the characters of the seed-stem zone, with the exception perhaps of the interseminal scales, which are at this stage of growth too small and indistinct to present clear outlines at so low an enlargement. They do appear in outline and would not be much clearer at higher enlargements.

The section affords the full equivalent of numerous serial sections of single seed stems and the seeds borne by them. Passing from the center of the section towards the periphery, the seed stems are cut further and further out, then the bases of the seeds, the mid-seed, seed apex and finally the extreme tips of the micropylar tubes as further illustrated in the succeeding photographs giving the necessary enlargements and better bringing out the strictly pentagonal ribbing of the seeds. It is interesting to find the ribbing of these very young seeds so much more pronounced than in later stages of growth, since we know this character to be primitive.

Photograph 3.—Cycadeoidea dacotensis. Section 927, Yale trunk 24. ×12. Enlarged views of seeds shown in preceding photograph.

Photograph 3a.—Cycadeoidea dacotensis. Supplementary section. ×10. Here the plane of the section passes out onto the surface of the strobilus, showing exact form of the seed tips and ends of micropylar tubes.

Photograph 4.—Cycadeoidea Wielandi. Yale trunk 393. ×2.15. Small ovulate cone borne on heavy peduncle and believed to have aborted after the dehiscence of a staminate disk. Note the darkly stained and probably wilted character of the tissues extending down to what may be an abscission line below the disk shoulder. This density of tissues is in strong contrast to the clear conservation of all adjacent structure.

Photograph 5.—Cycadeoidea Wielandi, Yale trunk 131. ×10. Mature seeds with well-conserved embryos. Observe the two cotyledons and even their bundle traces. (*Cf.* text-fig. 51.)

PLATE 21. *Cycadeoidea (minnekahtensis) Marshiana.* ×0.27. Rather young clump of short, compacted branches. Two views of Yale trunk 140. A Minnekahta, South Dakota, specimen. Weight 60 kg.

Except for the lesser fragments broken out near the summit and base on the fracture lines visible in both the upper and lower photographs, the present trunk is complete. The base, though not very well shown in the two views given, is nearly entire, the trunk being unusually broad and flat. In fact, the specimen is simply a mass of incipient branches, and it is quite clear that had growth proceeded, some full half dozen distinct leaf crowns would have gained the ascendency and produced a form of branching trunk like that shown in Volume I, Plates VIII and IX. This specimen is regarded as the finest example of a juvenile branching trunk amongst any of the habitually branched species thus far recovered. No fruits appear to view, and it is improbable that large polished surfaces would reveal even scattering fructifications.

PLATE 22. *Cycadeoidea (furcata) Marshiana.* ×0.44. An example showing bifurcation in a very large or predominant branch of a huge young clump.

One of the original types (Yale trunk No. 60) with large bifurcation, bearing various lesser lateral branches. The trunk is still young, no fruits appearing to view.

Branching in a plane, or simple bifurcation, with only small or suppressed lateral branches is of course the stage of branch growth intervening between the distinctly columnar trunk and the tuft type of branching seen in the *C. Marshiana* trunks fully illustrated in Volume I, Plates VII to IX. But such variations are in themselves insufficient characters for new species. (Compare with the bifurcate trunk, Vol. I, Fig. 11.)

PLATE 23. *Cycadeoidea Marshiana.* Yale trunk No. 129. ×0.33. An exceptionally handsome trunk just emerging from the pulcherrima or prefructification stage of growth. Minnekahta, South Dakota.

The leaf-base spirals are but little disturbed and only scattering fruits, mostly young, are present; also some small bract-enveloped branches are embedded in the ramentum.

The general trunk habitus is much as in *C. nana.* The central trunk remains distinct, bearing about its mid-periphery four large branches.

The plate size is scarcely sufficient to bring out all the surface details, but if a reading-glass be used, the small bract groups marking the incipient fruit series may be brought into view. (See photograph of opposite side given in the succeeding Plate 24.) On the side of the trunk opposite to the broken off branch *B* a large but as yet low branch has just begun to appear, as denoted by the arrow *B*, Plate 24.

The circle near the mid-height of the main stem denotes the position of a cylindrical core drilled out and sectioned, as illustrated on Plate 25. The large central bud in this core proved to be a young branch.

PLATE 24. *Cycadeoidea Marshiana.* Yale trunk No. 129. Complementary view to that of Plate 23.

In this view the branching appears somewhat more prominent, but it is especially interesting to find that the trunk symmetry is retained. The arrow *B* indicates a heavy branch which is just beginning to emerge in a position almost exactly balancing that of the branch of Plate 23 broken off. The other two arrows point out a few of the very young fruit axes as yet too little prominent to form a marked feature in a photograph of this size. Some of these grow close down in the angle between the branches.

PLATE 25. *Cycadeoidea Marshiana* and *C. Paynei* (?). Continuation of Plates 23 and 24.

Photographs 1 to 3.—Transverse sections 855, 874, and 868 cut at successively lower levels through the cylindrical core drilled from Yale trunk No. 129. For the exact position of this core see circle about half way up on main stem, Plate 23, on which the larger central bud plainly appears. The upper section, 855, appears to contain a peduncle at its center, but the bracts are over-large and probably pinnule-bearing, as observed in a somewhat similar axis cut from Yale trunk No. 210 (*cf.* Plates 38, 39, and 40). A little attention to the figures shows the quick change from the small U-bundle pattern to much fewer and heavier bundles at the insertion point of the leaf bases on the cortex, which is neatly traversed in section 868, photograph 3.

Photograph 4.—Cycadeoidea Paynei (?). Section 955, Yale trunk No. 399, cut through the armor about 3 cm. out from the cortex and 1 cm. beneath the surface. The general appearance and structure do not vary noticeably from that of photograph 1, section 855, but the leaf bases appear to be a little smaller. The spirals are slightly disturbed by young fruit growth, and it is of interest to observe the presence of two series of leaf bases, one larger and more numerous, the other smaller and considerably less numerous, but probably recurrent in groups. Two of these lesser bases, doubtless those of scale-leaves, appear at the upper right-hand edge of the photograph. Observe midway between the two leaf bases at extreme upper edge of photograph a minute ovulate cone just 3 mm. in diameter, which is, in the original section, quite distinct, although the seed-stem zone is markedly under a millimeter in thickness.

Photograph 5.—Cycadeoidea Marshiana. Yale trunk 744, section 890. Characteristic armor section agreeing precisely with section 855, photograph 1.

PLATE 26. *Cycadeoidea Marshiana.* ×0.43. Yale collection, No. 3, Minnekahta, South Dakota. View showing drill-holes and a small cavity at *B* due to breaking out or non-conservation of a small branch.

This trunk bears various ovulate fruits which have just shed staminate disks. The flowers were probably all "complete."

The larger drill-hole yielded a core containing three ovulate fruits (text-fig. 19) and the smaller, beneath the cavity *B*, the bisporangiate strobilus of text-figures 16, 17. The arrows, some 14 in number, locate various additional bract-inclosed axes, and many others are present. It appears that most if not all these fruits belonged to a single fertile period.

PLATE 27. *Cycadeoidea Marshiana.* Illustration of Yale trunk No. 3, continued from preceding plate. Photographs of cylindrical core sections supplementary to text-figures 16 to 20.

Photographs 1, 2.—Two transverse sections of core I. Natural size. The section, photograph 1, traverses the armor about 5 cm. distal to leaf-base insertion; three ovulate cones are cut. The dark center of the middle cone is merely the transversely cut elongation of the parenchymatous cushion, and not a small seed cone surrounded by staminate tissues, as might be suspected even when viewing this illustration under a reading-glass. In photograph 2 the peduncles of these cones appear, the most interesting feature being the clear disk annulation surrounding the extension of the peduncle bearing the ovulate cone. To bring out this disk annulation so clearly the section had to fall at exactly the right level, which it did by fortunate chance. A millimeter higher or lower would have left the annulation obscure or out of view entirely.

Photographs 3, 4.—Sections 723 and 725, cut from core No. IV. ×2. These two sections effectively supplement photographs 1 and 2 in the illustration of cone features as seen in transverse section.

Photograph 5.—Longitudinal section 728, cut from cylindrical core No. III. ×5. At this enlargement the relatively heavy disk annulation becomes distinct. Both in the illustration and in the section itself there is a strong suggestion of developing periderm that would eventually have resulted in cone abscission had the normal course of growth continued. But the preservation of minuter details is not so perfect as to enable one to judge clearly the exact meaning of the appearance here presented; for the ordinary course of silicification might easily result in just such symmetrical color zones limited by more or less deceptive agatizations. However this may be, the very frequent recurrence of what appears to be an abscission zone both in the case of very young cones which may have aborted after maturing their disks and of mature seed cones is worthy of notice and doubtless can be in the course of time explained more precisely than now. (For further illustrations of core sections from trunk No. 3, see the series of text-figures given in the general description of *Cycadeoidea Marshiana.*)

PLATE 28. *Cycadeoidea pulcherrima.* Cylindrical core sections and apical bud. The core was cut from a trunk weighing about 40 kg. and one of the very finest examples of the prefructification or pulcherrima stage of growth. The actual species to which this trunk should be referred remains in doubt, but it may be a *C. nana.* All photographs natural size. [Photographs 1–4 only.]

Photograph 1.—Armor surface of the core, which gives but a slight indication of the very ornate character of the leaf-base spirals.

Photograph 2.—Polished saw-cut a full centimeter and a half beneath the preceding surface. Coming from the same core segment which yielded photograph 1, the leaf-base spirals are of course shown in reverse, that is, left-right order. But in this trunk the left-right and right-left spirals have so nearly the same angle, and the leaf bases, despite their varying form and angles, change so evenly first towards one and then towards the other side, that the reversal of the spirals is hardly appreciable.

Photograph 3.—Transverse section cut from somewhat lower down than the polished section (S. 759).

Photograph 4.—Section 758, from a still lower level, showing unexpected persistence of the small size of the leaf bases. It appears that many scale-leaf bases may be present, it being quite possible that only a minority of the fronds actually bore normal pinnule series. Observe that photographs 3 and 4 show the spirals in reverse order.

Photograph 5.—Cycadeoidea (Cycadella) Wyomingensis. Polished surface traversing an isolated terminal bud exhibiting the same type of preservation and leaf-base form as the preceding sections.

Photograph 6.—Cycadella Reedii type. Base of trunk showing the small-sized, relatively heavy woody cylinder. The leaf-base spirals are scarcely evident, but a transverse section would disclose the same regularity seen in the foregoing sections. Natural size.

PLATE 29. American and Isle of Portland Cycadeoideas. All natural size.

Photograph 1.—Cycadeoidea Wielandi, Yale trunk 131, section 965. Depressed or oblique section through wood cylinder and cortex, showing spiral order of both the cylinder meshes and cortical traces, here undisturbed by peduncle traces.

Photographs 2, 3, 4.—Cycadeoidea (sp.), probably *C. Marshiana.* Successive transverse sections from a cylindrical core cut from a Yale trunk fragment (No. 479). Sections Nos. 885, 879, and 888, the latter passing through the inner cortex and showing the origin of the cortical traces.

Photographs 5, 6.—Cycadeoidea microphylla. Transverse sections through cores drilled from Yale specimens 800 and 803, of the general type illustrated on Plate 3, photographs 4 and 5. Photograph 5 shows a core from trunk 803, in which the *microphylla* type of leaf base forms the characteristic spirals of the pulcherrima stage of growth, but a single small peduncle appearing in this section. Obviously, conservation is not equal to that of the better conserved Black Hills trunks. Yet these are fine Cycadeoids and would, with patience devoted to their study, afford excellent material for histologic comparison. In the section shown in photograph 5 the ramentum is remarkably well conserved over large areas, being one cell thick, as in *Cycadeoidea etrusca* and other Italian specimens, as well as in some Black Hills forms. Also the outer sclerodermal layer of the leaf bases is very distinct; likewise the palisaded hypodermal parenchyma. Parts of the bundle xylem clearly outline the *Cycadeoidea* pattern, and there is much development of bands of excising periderm.

In photograph 6 the leaf-base spirals are much thrust aside by emergence of both fruits and branches (?). For drawings of similar sections see text-figure 39.

PLATE 30. Woody Cylinder and Armor Features of characteristic American and European silicified Cycadeoids. The trunks illustrated on this plate are all very distinct and afford a basis of comparison at once interesting and usable in determining species.

Photograph 1.—Cycadeoidea Paynei. Section 981, natural size. This section is one of those cut from the U. S. National Museum type, one of the three or four most perfectly silicified Cycadeoids ever sectioned. The wood zone is moderately thick, the phloem well developed, but less in amount than the xylem; the cortex has a medium development.

Photographs 2 to 4.—Cycadeoidea nana (?). This small trunk segment, shown natural size in transverse (photograph 2), radial (photograph 3), and tangential section (photograph 4), would be referred to *C. rhombica* were it not for the presence of groups of lesser or scale-leaf (?) bases. The large pith, the thin wood zone equally divided between xylem and phloem, and thin cortex with well-marked one-strand leaf supplies, are the outstanding specific characters. Observe in photograph 4 the peduncles of two sizable fructifications. The conservation of this specimen is far less perfect than in *C. Paynei,* but all larger features stand out more boldly, the polished surfaces yielding as good photographs as the thin sections. The surface of photograph 2 is exactly transverse to the upper border of that of the radial section, photograph 3; and the armor section, photograph 4, forms a right angle with the radial section, photograph 3. The somewhat abnormal thinning out of the wood zone noted in photograph 2 may indicate that this trunk segment is a part of a branch.

Photograph 5.—Cycadeoidea etrusca type (Capellini Museum, Bologna). Leaf-base section. ×2.15. Preservation exceedingly good, but a little obscured by the presence of finely disseminated iron or perhaps residual carbon (?).

Photograph 6.—Cycadeoidea megalophylla. Natural size. Polished transverse surface of basal segment of one of the characteristic trunks of the Portland "dirt bed." The photograph gives nearly the true color value of the polished surface. The height of this section above the trunk base is about 10 cm. Medulla large; wood well developed, as in *Cycadeoidea Dartoni;* xylem-phloem proportion 3 to 1; cortex nearly as broad as wood zone, and leaf bases very large, even 4 to 5 cm. across.

Photograph 7.—Bennettites Gibsonianus type. Transverse section of leaf base near armor insertion. Enlarged three times. The photograph has been accidentally inverted. This is one of the types with a thin wood zone and thick cortex. The large size of the leaf-base bundles merely indicates rapid union at this point to form the single cortical strand of lunate or horse-shoe transverse section. Like *C. etrusca* the Isle of Wight type exhibits remarkably fine conservation, with some darkening due to iron or carbon.

PLATE 31. *Cycadeoidea Wielandi.* Armor, cortex, and woody cylinder features of the two Yale trunks No. 77 and No. 393, both of which are typical for this species. See photographs of trunk 77, reference 373, plate 111, photograph 1, and 357, Plate CXVI; the photograph of trunk 393 is given in Volume I, Plate XXI. See also various text-figures of Volume I, and the present text-figures 29–34.

Photograph 1.—Section 949, trunk 393, transverse section through leaf bases near insertion on cortex.

Photograph 2.—Section 924, trunk 393, obliquely depressed section through the cortex, showing the spirally arranged crescentiform sections of the leaf traces with interspersed strands which go to form the cylindrical peduncle traces.

Photograph 3.—Supplementary to preceding (section 953, trunk 393), showing xylem and phloem of woody cylinder.

Photograph 4.—Another section cut through the cortical region, enlarged twice. Trunk 393. Observe that such sections through the cortex must often be characteristic for a given species. The size of the leaf traces is more or less proportional to that of the leaf bases. The oblique cortical section is an important supplement to the leaf-scar spirals.

Photograph 5.—Transverse section through woody cylinder and cortex, showing emergence of the leaf trace. Enlarged three times.

Photograph 6.—Radial-longitudinal section through woody cylinder and cortex, showing the origin of the leaf traces on the woody cylinder and passage outward and upward through the cortex into the leaf bases. Division into strands on splitting up into leaf-base bundles of course begins in the outermost cortex. (Section 948, trunk 393. ×1.)

Photograph 7.—Another radial-longitudinal section traversing woody cylinder, cortex, and armor, with embedded seed cones. (Section 936, trunk 77.) It may be noted that the sections illustrated on this plate, although cut from two different trunks, show the same type of preservation. There is not the slightest doubt that the trunks are of the same species. The section series could have been made equally complete from either one of the trunks.

PLATE 32. Cortex and Armor Features of *Cycadeoidea.* A continuation of the preceding plate.

Photograph 1.—Cycadeoidea Wielandi. (Section 891, trunk 77. ×1.) Representative thin section through mid-region of armor, traversing the peduncles of various mature ovulate cones and also those of several of the series of small or aborted ovulate cones.

Photograph 2.—Section 964, Yale trunk 77. ×2. Obliquely depressed transverse section through woody cylinder, cortex, and armor. An especially characteristic section, the features of which should be studied *seriatim*, beginning at the woody cylinder and passing out to the armor. The depression of the section was carefully estimated so as to cut the leaf and peduncle traces as nearly transverse as possible, and in nearly all of the cortex there is little departure from the true transverse section of the traces. Note the spiral order of the horseshoe section of the leaf traces as they emerge from the cylinder; then observe that interspersed strands appear, several of these latter uniting to form the large axillary peduncle trace, which at last assumes a flattened cylindrical form. Note that 3 peduncle-trace sections are a prominent feature, the first appearing in the mid-cortex, the second at the outer edge of the cortex, and the third in the basal armor region. From this section alone it is quite clear that the peduncle trace is composed of a right and left strand, perhaps comparable to the right and left strand which finally makes up the leaf-base bundle supply in existing cycads. These are virtually serial sections.

Photograph 3.—Cycadeoidea Wielandi. Section 951, trunk 393. ×1. Supplementary to preceding photograph.

Photograph 4.—Cycadeoidea megalophylla. Transverse section through woody cylinder of an Isle of Portland specimen. Natural size. As may be judged from the appearance of this thin section, the Portland trunks were more subject to maceration than the finely conserved specimens from the Black Hills. Nevertheless, the histologic features permit critical study. Note presence of the so-called "growth rings."

Photograph 5.—Cycadeoidea superba (?). Transverse section 963, trunk 744. ×1. This section traverses the cortex somewhat obliquely, just as that shown in photograph 2, and finely illustrates the variations in the cortical bundle system observable in widely different species. The outer edge of the phloem appears above, the leaf bases below.

PLATE 33. Woody Cylinder Features of Isle of Wight and Black Hills Cycadeoideas.

Photograph 1.—Bennettites Gibsonianus. Radial longitudinal section through inner xylem of original type. Tracheids with rather shallow scalariform marking adjoining large pith cells of the medulla. Within the wood zone are the squarish tabulate pith cells characteristic of the woody cylinder meshes of all existent and fossil cycads. The scalariform marking which characterizes the tracheidal tissue is comparable in appearance and partly in conservation to that of *Cycadeoidea (Cycadella) wyomingensis.* It is more pronounced in other sections, extending all the way to the cambium.

Photograph 2.—Bennettites Gibsonianus (type.) Correspondent transverse section to preceding. At the lower edge of the photograph the outer medulla appears, also the isolated tracheids at the inner edge of the wood. The square outlines of the lesser ray cells are very evident.

Photograph 3.—Cycadeoidea Dartoni. Section 1008. ×100. Tangential section through xylem.

Photograph 4.—Cycadeoidea Paynei. Section (type). ×100. Tangential section through xylem near a woody-cylinder mesh. Note peculiar wall-thickening of the ray parenchyma cells. To a lesser extent this feature is present in *Bennettites Gibsonianus, Cycadeoidea Dartoni,* and doubtless most fossil Cycads. In some species it is only developed in the inner xylem region. These rather peculiar ray cells are paralleled in certain Cretaceous conifers, and curiously enough, appear to have been a gymnosperm character of Cretaceous rather than later time.

PLATE 34. Wood Structure of *Cycadeoidea.*

Photograph 1.—C. Dartoni. Section 1008. ×200. Tangential section through xylem, showing the radial wall pitting of occasional slightly twisted tracheids.

Photograph 2.—Supplementary to preceding. Same section and enlargement. Observe that it is here scalariform rather than pitted sculpture that comes to view. These are both selected areas.

Photograph 3.—C. Paynei (type). Radial longitudinal section through inner xylem. ×190. A selected area containing scalariform, pitted, and spiral tracheids. The spiral tracheids grade into scalariform, and the latter into pitted forms. Such tracheid gradation is a well-known feature of the ancient gymnosperms, especially *Cordaites.*

Photograph 4.—C. Paynei (type). Tangential section through phloem. ×90.

PLATE 35. Wood Structure of *Cycadeoidea* (continued).

Photograph 1.—Bennettites Gibsonianus. ×100. Transverse section through phloem.

Photograph 2.—Same as preceding, but showing xylem, imperfectly conserved cambial layer [partly cut out], and phloem. Observe approximate equality in size of the outer xylem tracheids and the thick-walled phloem elements, comparing with photograph 3.

Photograph 3.—Cycadeoidea Paynei (type). Transverse section through woody cylinder on cambial layer. Here there is disparity in size between the outer xylem cells and the thick-walled inner phloem cells. How far this character may be diagnostic of species is as yet unknown, since the possible variation in any given trunk has never been studied.

Photograph 4.—Cycadeoidea Paynei (type). ×190. Radial longitudinal section through xylem, showing transition from scalariform to slit and pitted sculpturing; also transition from spiral to distinctly scalariform marking.

Photograph 5.—Cycadeoidea Paynei (type). ×100. Supplementary to preceding.

Photograph 6.—Cycadeoidea Dartoni (type). Radial longitudinal section through outermost xylem, showing nucleated medullary-ray cells, and well-developed scalariform marking of the tracheids. The appearance of the ray cells is precisely such as may be observed in existing cycads.

PLATE 36. Wood Structure of *Cycadeoidea* (continued).

Photograph 1.—Bennettites Gibsonianus (type). Transverse section through xylem, showing several especially heavy parenchyma rays. Some wood parenchyma is present, but does not appear very plainly in the photograph.

Photograph 2.—Cycadeoidea Dartoni (type). Transverse section through xylem. Lesser medullary-ray cells with same wall-thickening observed in *C. Paynei* (*cf.* photograph 5).

Photograph 3.—Cycadeoidea Dartoni (type). Transverse section through xylem. This wood is quite characteristic, the tranversely cut tracheids appearing to vary more and to be more angular than in most forms, while every here and there a rosette-like group of cells surrounds a thin-walled element.

Photograph 4.—Cycadeoidea Paynei (type). Transverse section through inner xylem, showing extensive development of marked medullary-ray cells. Dark ray cells doubtless resinous.

Photograph 5.—Supplementary to preceding, showing wood parenchyma to left.

PLATE 37. *Cycadeoidea nana* (*?*). [×0.35.] Obverse lateral views of a branching specimen obtained from *in situ* position by the author at Minnekahta, South Dakota, in 1902.

Four branches rise from the main central stem, which first gave rise to the two low-set and large basal branches numbered II and III, these being followed by the lateral branches I and IV. That numbered IV is the smallest and fails of the good preservation seen in the others.

Near to branch IV the central stem also bears a small but finely conserved ovulate strobilus indicated by the arrow *O. S.*

This handsome specimen has an added interest as one of the few trunks found in place in the Black Hills. It lay on its side, embedded in a characteristic stratum of straticulate clayey sandstone bearing traces of foliage imprints, and but a few square centimeters of the lateral surface of the stem could be seen. It is from the same horizon and near the same point as large trunk of Plate V, Volume I.

Had this unusually interesting specimen been eroded out like most American and the Italian Cycadeoideas, the basal branches, which were already fractured across their junction with the main stem, would have become separated and most probably could never again have been recognized with certainty as pertaining to one and the same plant; much less could they have been brought into their natural position.

PLATE 38. *Cycadeoidea Dartoni* (*?*). [×0.375.] Trunk from Minnekahta, South Dakota, which bears several short lateral branches, various nearly full-sized ovulate strobili, and a very numerous series of young strobili. Yale specimen No. 210.

The striking similarity of this trunk to the Hermosa cycad will at once be noted. With that specimen there is a close agreement in general size and form of the main stem and its terminal bud, as well as leaf bases, bundle development, and pattern, together with volume and structure of both frond and bract ramentum. So, too, the larger ovulate strobili agree fairly within specific limits. But the wood zone is unstudied, and the presence of distinct branching as opposed to total absence of branches in the Hermosa cycad must be taken into account. The even growth of the remarkable embryo-bearing fruits in the latter, appears to denote a striking variation from the present trunk with

fruits belonging either to two seasons of fruit production, or else to fruits of two maturation series, the one, with or without stamens, and maturing seeds, the other staminate with abortive seed cones. However, if the lesser series is analogous to the older it would represent merely the main or culminant fructification, exhibiting, if so explained, a variation from true monocarpy within the species; while similarly the lesser lateral branches in any case whatsoever constitute a visible transition from columnar to much-branched forms. It is of much interest to find that at the trunk base the fruits are sparse and the leaf bases relatively larger and more prominent, with fewer scale leaves than at the summit, where the fruits are abundant. Had the base of the trunk only been recovered the strong resemblance to *C. Dartoni* type would be obscured. But these various points must be interpreted by later studies. (Compare Plates 39, 40, and 52, photograph 2.)

PLATE 39. *Cycadeoidea Dartoni* (*?*). [×0.365.] Yale trunk No. 210 viewed from side opposite to that shown in the preceding plate.

In this view the tendency to the columnar trunk form appears more pronounced and there is brought to view the rather curious fact that on this side of the trunk with the armor mass uninterrupted by branches a considerable number of the fruits are further advanced in growth than on the opposite branched side seen in the preceding plate. Some of these secondary axes, however, bear young fronds and are incipient branches just like the old buds of *Cycas*. The trunk is clearly not so tall as the Hermosa cycad must have been. The arrow and ellipse show the exact position from which was drilled cylindrical core No. 11, illustrated on the succeeding plate.

PLATE 40. *Cycadeoidea Dartoni* (*?*). Yale trunk 210. Sections through cylindrical cores I and II, drilled from the position indicated in plates 38 and 39. Photographs are natural size, except No. 5, which is enlarged three times.

Photographs 1 to 3.—Transverse sections through drill core I (*cf.* Plate 38), cut at successively lower levels. Two series of fruits are evident in photograph 1, both being ovulate. The condition present may indicate an early sparse series of ovulate fruits followed by a much more numerous series of a succeeding season. As there is no evidence of staminate forms so far, a dicœcious condition seems probable; but in order to determine the true nature of these flower-buds every individual cone and bud would have to be studied over larger areas than appear in this section. One of the interesting features is the small size and flattened-out condition of the leaf bases, which are markedly larger towards the base of the trunk. This condition suggests that as the trunk approached the period of active fruit production, the fronds tended to attain only the medium size or also dropped gradually back to mere scale-leaf size. Perhaps much the greater number of the bases are those of scale leaves or of fronds with few pinnules. A further and less likely explanation is that as the period of active fruiting began there was considerable resorption of the leaf-base substance with resultant wilting. This idea is tentatively given in connection with the description of armor features illustrated on Plate 45, where these same peculiarities recur. An enlarged view of the most interesting portion of this section is given on plate 52.

The features of photograph 1 may easily be traced in photographs 2 and 3, despite the fact that the sections were inadvertently photographed from the reverse side. In both the sections the larger and smaller peduncles clearly appear.

Photographs 4 and 5.—These show the transverse section of cylindrical core II (*cf.* plate 39) in the natural size, with the complementary longitudinal section cut on the line *ss*, enlarged three times. That is to say, the base-line of section 858, photograph 5, falls at only a saw-cut distance from the plane of the transverse section, photograph 4. The features of this longitudinal section are noteworthy. The large central axis proves to be a somewhat asymmetrical branch and the transverse sections through its summit reveal the presence of the folded ranks of young pinnules attached to their small petioles, at first taken for bracts. Above this branch are the two young ovulate cones with elongate parenchymatous cushions instead of the short convex cushions which characterize the full-grown ovulate cones. It will be recalled that short and long cushions are features of the ovulate and staminate fruits of *Cycadeoidea Jenneyana*, a very different species from the present, and obviously monœcious. Here, however, the evidence is less clear, and further sections are required. The somewhat elongate cushions might in later growth stages assume the convex form.

PLATE 41. *Cycadeoidea Dartoni* n. sp. ×0.33. A monocarpic trunk in full fruit, between 500 and 600 ovulate cones being present, the greater portion in a remarkably perfect state of preservation. From the Black Hills "rim," about 6 miles west of Hermosa, South Dakota. Discovered by N. H. Darton, of the U. S. Geological Survey. To the illustration of this extraordinary specimen the series of Plates 41 to 50 is devoted. In this initial plate the quarter view from the most eroded side and the longitudinal section are shown in about a third the natural size. The complementary armor view from the opposite and uneroded side is given by photograph 1 of Plate 42, and the longitudinal trunk section is again represented in the natural size on the double Plate 43.

On scanning the armor surface to the right the cavities left by some broken-out fruits are noted. In other cases portions of the fruits are still present; in still other and numerous instances nearly all of the fruits except the apical bract husk is conserved. Very nearly the normal condition of perfect conservation is exhibited by the armor on the opposite side of the trunk (Plate 42, photograph 1), where the closely packed cones lie deeply embedded in the armor,

hidden from view by the enveloping dense mass of hairy bracts, forming a nearly flat surface. While the abundance of cones is here much more in evidence than in the complementary view of the opposite trunk surface, neither of these views, and much less both taken together, would in the absence of the transverse armor sections reveal the fact that the half segment alone bears 300 cones. In fact, owing to the light ashy-gray color of the trunk itself, mainly due to a thin coating of lime, the great number of fruits would scarcely be suspected without the most careful examination of those areas on the original specimen where the densely packed bracts are most eroded away or where some of the fruits have been broken out during the process of erosion from the matrix in which the trunk was embedded.

PLATE 42. *Cycadeoidea Dartoni* type. Continuation of Plate 41.

Photograph 1.—Half of trunk segment from best conserved side. The right edge of the photograph thus marks the left side of the complete longitudinal section of the trunk shown in the natural size on Plate 43. The view is about one-third the natural size. The white color about the trunk base is mostly due to a thin incrustation of lime; but armor and bract preservation is complete over nearly all the surface of the lower half of the trunk segment. No cone apices appear at the surface, the fruits being everywhere overtopped by the leaf bases and bracts. Towards the apex of the trunk conservation does not extend quite so far out, and the partly eroded ends of some 30 of the cones may be counted. In this upper portion of the armor the cones, although still very abundant, are less densely packed than in all of the basal region. This photograph affords the key to the position on the trunk of the transverse trunk sections shown on Plate 44. The areas and positions of the principal transverse sections through the armor are indicated by the plate numbers 45 (1); 46 (4); 47, on which the sections are severally illustrated. Reference to these plates shows the character of the cones from the base of the trunk segment nearly to the apex of the trunk.

The numbers 1 to 6 in the area of the section marked XLVII denote cones which may be seen at the trunk surface. Nearly all the cones below the level of these are deeply hidden in ramentum. These cones are similarly numbered in Plate 47, which is photographed in reverse. They also appear in direct position (photograph 6, plate 45).

The arrow to the left near the trunk apex denotes the level of a large transverse section passing through scattering small cones 1 cm. or less in diameter. It was originally intended to illustrate this very interesting section as Figure 3 of the present plate, but owing to the very dark natural staining at this level the photographs proved too dense for successful reproduction. Inasmuch as this section is one of a series displaying most satisfactorily the entire anatomy of the crown apex and terminal bud, it may be made the subject of future illustration.

Photomicrograph 2.—Section 1007. ×7. Transverse section through outermost cortex, traversing woody cylinder of a peduncle and the crescentiform traces of the subtending leaf base. Observe that at this point the leaf trace is made up of two very large crescentic bundles, each of which gives rise to a lesser inner bundle of nearly normal leaf-base size. But a few millimeters further out the large traces would be found divided into very nearly the normal number of leaf-base bundles aligned in characteristic pattern. Very near the origin of the leaf strand on the trunk the axillary peduncle bundle is found to take its origin as several branches. It is thus seen that while the single leaf-base strand divides up in the outer cortex, the peduncle strand results from fusion in the inner cortex in the true axillary position. It is very probable that the peduncle strands are so distinctly fused with the leaf-base trace that more or less resorption of leaf-base tissue goes on during cone growth. (*Cf.* photograph 3; also photograph 7, Plate 30, which shows how the two heavy strands may persist well out into the leaf base before the final subdivision.)

Photomicrograph 3.—Section 1005. ×3. Transverse section parallel to preceding, traversing the mid-cortex, where both leaf-base, and peduncle bundle strands are single, the former being characteristically crescentic, and the latter uniformly cylindrical. The xylem, cambial line, and rather dense phloem zone are alike unmistakable.

Photomicrograph 4.—Section 985. ×3. Transverse section through ramentum mass forming the extreme apex of the trunk. The photograph shows alignment of the ramentum corresponding to the terminal bract helicoid, although at this level no bracts are cut. The alignment of the ramental scales appears so sharp because of the heights at which the scales are, as the result of uniform growth, unfailingly cut. This produces a stippling or shading effect nearly as pronounced as if the bracts themselves were transversely cut. At this enlargement the individual scales just begin to appear, but the two preceding photographs are not sufficiently enlarged to bring out the remarkably conserved histologic structure.

PLATE 43. *Cycadeoidea Dartoni* type. Continuation of Plate 42. Longitudinal section through upper segment of trunk, displaying many fruits and the medulla, woody cylinder, cortex, and armor. Natural size. The plate is folded at the level of the transverse saw-cut which yielded the polished surface shown on the succeeding plate.

As will be observed on reference to the succeeding plate, the present polished surface is on the short diameter of the elliptical section resulting from trunk compression. Consequently both cortex and medulla appear to have only half their true dimensions, just as they would, on the contrary, appear about twice as extensive as they actually are were the section cut on the long diameter of the elliptical section of the trunk.

About the only other result of compression evident is the sharper angle of the leaf and peduncle traces and the slightly greater droop of the strobili. In a longitudinal section cut at an angle of about 45° to the present section the nearly true proportions of the medulla and cortex must obtain. So, too, the position of the fruits and leaf bases and their cortical traces must be nearly the original normal one.

The conservation in the lower half of the section not being so good as further up, the full size of the woody cylinder is not at first clearly evident; but on closer study it is seen to hold its development evenly and diminish regularly in thickness all the way to the apex of the trunk.

On the left side of the trunk 20 fruits may easily be counted and traces of many more made out. On the right side, owing to erosion, only the peduncles and a few basal portions of the fruits remain.

Obviously *Cycadeoidea Dartoni* is a narrow-cortex, heavy wood-zone type. If the full height of the trunk was 1 meter, a moderate estimate, and the steady increase in the thickness of the woody cylinder was maintained all the way to the base of the trunk, as it would be and a little more, the thickness of the woody cylinder near the base would be 3 cm. But the actual thickness may have been more.

In the medulla numerous secretory sacs appear instead of the more elongate gum canals characteristic of modern Cycads. The sacs are reported in much smaller stems. (Reference 13, page 78.)

PLATE 44. *Cycadeoidea Dartoni* type. Continued from Plate 43. Transverse section of half of trunk, shown in the natural size.

In this unusual section 11 complete fructifications appear, 6 other cones being cut less favorably. Six of the entire cones are cut in nearly median longitudinal section. The fruits can not be here cut in exactly the median longitudinal section, because of their droop in the armor.

The armor, cortex, woody cylinder, and medulla all appear in exact outline and proportion. The woody cylinder is 2 cm. thick, the proportion of xylem to phloem being as 3 to 1.

Most noteworthy are the results of trunk compression. The flattening of the medulla produces little observable distortion, while neither the woody cylinder nor the fruits are appreciably altered in form. It is in the cortex as traversed by the leaf and peduncle traces that the effects of compression are most marked. As will at once strike the eye, the cortex shares about equally with the medulla in the flattening of the trunk, being more than twice as thick in the horizontal as vertical plane. The proportions are 1.5 cm. to 4 cm., indicating a cortical thickness of very slightly less than 3 cm. As will be noted when studying supplementary sections, the actual length of the cortical leaf and peduncle traces remains unchanged, compression decreasing the axillary angle in the vertical and increasing it in the horizontal direction, so that these strands pass out at nearly a right angle where the cortical parenchyma is broadest.

Further pressure would of course have resulted in breaking up of the cortical region, so that it would even appear that the cortical strands when pressed out into the position vertical to the trunk possessed sufficient strength to stay further distortion in the matrix. Compression before mineralization is the best explanation of the condition found.

PLATE 45. *Cycadeoidea Dartoni* type. Continuation of Plate 44. A series of transverse sections through the outer armor, showing the great abundance of the seed-bearing cones, with the relatively small number of small or young axes not bearing well-conserved seeds. All the photographs are shown natural size.

On Plate 42, photograph 1, the position of the sections shown by photographs 1, 3, 4, and 6 is definitely indicated. The interesting point to note is that these sections are tandem to each other, extending almost continuously from the trunk-segment base to within 20 cm. of the summit. These four sections thus traverse the zone of closely packed fruits for a distance of 35 cm. along the trunk, with the exception of a few centimeters lost by saw-cuts. The cones continue abundant for a distance of 6 to 8 cm. above the upper edge of the field of photograph 6, although smaller as they thin out at the base of the terminal bud.

Photograph 1.—Transverse section of hand specimen broken off base of trunk for the preliminary study (*cf.* synonymy, 1911).

Photograph 2.—A section exactly parallel to the preceding cutting the bases of the cones. In the middle cone convex cushion is cut. These smaller sections show to somewhat better advantage the leaf bases, no more numerous than the cones themselves.

Photograph 3.—A large polished surface from base of trunk (*cf.* Plate 42). Before photographing the dark polished surface was glossed to bring out the surface details. As this is the surface of the slab *sawn from* the trunk, leaf spirals are of course reversed. Only two axes not bearing seeds may be seen. Eighteen cones with well-conserved seeds are cut. This is the large area marked XLV, 1 on Plate 42, photograph 1.

Photograph 4.—Section 1001. For enlarged view see Plate 46.

Photograph 5.—Enlarged view of a portion of another polished surface traversing the cones. This view shows especially well the color values of the polished surface and the large proportion of seeds containing the dicotyledonous embryos, but the enlargement is not quite sufficient to bring out embryo features sharply.

Photograph 6.—Thin section cut from a still higher position on the trunk (*cf.* key photograph 1, Plate 42). Although a full dozen well-conserved seed cones are cut, only one small or aborted axis appears. (For enlarged view of a parallel and more basal section see Plate 47.) The position of fruits 1, 2, 3, and 5 on the trunk is indicated by these corresponding numbers on photograph 1, Plate 42.

PLATE 46. *Cycadeoidea Dartoni* type. Continuation of Plate 45. Section 1,001, enlarged three times.

In this section 10 strobili are in whole or part visible, and but 8 leaf bases, while the interesting fact is brought out that the strobili are by no means uniformly axilar to the leaf bases, as usually observed. In the upper middle portion of the field of the section 6 leaf bases are surrounded by 7 well-grown cones; but where so many fruits emerge all over the trunk surface the relation of the individual fruits to the adjacent leaf bases may come to be more or less obscured, so that some of these fruits may be much more nearly axilar than they appear to be.

The seeds with the dark interiors are much the best conserved and uniformly contain mature embryos. The lighter colored seeds are also mostly fertile, seed coloration varying considerably even in the same cone.

It is well to compare this section with section 887 of Yale trunk 210 (Plate 52, photograph 2). The study of trunk 210 was carried out before *C. Dartoni* was discovered, it being suspected that the species was new. Slight differences in the size of the seeds and outer envelope of sterile scales are explained by the small number of seeds in the more or less isolated cone of section 887, analogous differences being common in seed-bearing plants. The full meaning of the second series of fruits in section 887 (assuming that the woody-cylinder structure of the trunks is in agreement) is more difficult to explain. But it is easily conceivable that individual trunks may have been inequally monocarpic. At least there does not appear to be sufficient reason for regarding these forms as separate species because of this difference alone.

PLATE 47. *Cycadeoidea Dartoni* type. Continuation of Plate 46. Section 983. ×2. (For position on trunk see key photograph 1, Plate 42.)

Although situated much further towards the summit of the trunk than the preceding cone sections, the present armor section still lies within the zone of abundant fruits. Sixteen seed-bearing cones lie wholly or in part in the field of this section, two further axes marked by arrows apparently having failed to reach maturity. The bracts of these axes are large like those of the cones.

The leaf bases, which may not number more than 18, are for the greater part not well conserved at the level of this section. There is even a suggestion that the leaf bases were subject to considerable wilting or even resorption during the period of active fruit growth. At the height of this section the individual cones still retain very nearly the average size seen much lower down on the trunk; but within the next 5 cm. diminution in size becomes marked, and a little higher still the cones begin to thin out.

This section is photographed in reverse view (left-right) or just as one would see it *if seen in normal position from the axis of the trunk*. For this reason the cones marked 1 to 6 do not at first appear to correspond to those numbered similarly in the key photograph of the trunk (photograph 1, Plate 42) and in the section of photograph 6 of Plate 45. But they are precisely the same cones, as may easily be made out by giving the least attention to the grouping.

PLATE 48. *Cycadeoidea Dartoni* type. Section 990. ×2.3. Radial-longitudinal trunk section traversing woody cylinder, cortex, and armor.

This striking thin section was cut from the upper left-hand portion of the lower trunk segment of Plate 43. It traverses 2 fruits in a nearly true median plane and cuts 3 others tangentially. As seen in the 2 superposed fruits, the heavy peduncles arise from the axils of the leaf bases, which appear to have been thrown somewhat forward as the cones reached their full size. Obviously it would require several such sections to bring out to the best advantage the axillary connection between the leaf and peduncle trace. In all probability there is no difference in relation between a peduncle which originates in the leaf-base axil at the inner border of a heavy cortex and a flower-bud supply of a dicotyl which originates in a leaf axil enveloped in a very thin cortex.

The phloem *appears to have split away from the xylem cylinder* somewhat, leaving the broad band which traverses the entire length of the wood in the cambial position. The hard wood has about three times the development of the sap wood, and growth rings are as numerous and pronounced as they might be in some dicotyl. The *compressed* cortex has about twice the thickness of the sap wood. (For tangential cortical sections see Plate 42, photographs 2, 3.)

PLATE 49. *Cycadeoidea Dartoni* type. Transverse and longitudinal sections through cone. Enlarged 3 and 10 times respectively.

Photograph 1.—Transverse section through armor fragment broken from the base of the type (*cf.* Plate 43). The dark centers of the seeds indicate the conserved embryos. Relatively few of the seeds are infertile. Sec. 897.

Photograph 2.—Nearly true median longitudinal section through upper portion of cone. The section passes out somewhat obliquely on the right side. Nevertheless, three of the small micropylar tubes are cut through their full length. Compare with cone of Plate 51, showing seed type with heavier basal development of "blow off." Sec. 907.

PLATE 50. *Cycadeoidea Dartoni* type. Transverse section of seed cone, enlarged 10 times. Supplemented by the succeeding plate, which shows longitudinal section.

In this view, owing to the oblique position of the seeds, an extended series of slightly oblique seed sections passing from the base to the extreme tips of the micropylar tubes may be observed. The dense woody envelope formed by the nailhead-like ends of the interseminal scales is a striking feature.

PLATE 51. *Cycadeoidea Wielandi.* Longitudinal section through ovulate cone, enlarged 10 times to show seed stems, seeds, and especially surface features and the micropylar tubes.

On the left side of this photograph for a considerable distance up the side of the cone the actual outer surface clearly comes into view. The extreme ends of the micropylar tubes are seen to be surrounded by the ends of the interseminal scales. Several tubes are cut longitudinally and just above them a number of the tubes are seen to be cut at varying distances beneath the extreme ends. These tubes are cut nearly in the transverse direction, and it is of interest to observe that the sections are pentagonal, indicating a symmetrically 5-ribbed seed. In one seed this pentagonal character is evident. The fact that the two uppermost angles fall close together is due to the obliquity of

the section, which passes from just above the seed base on the one side to the shoulder region of the opposite side. And so may be explained the features and outline of every seed. Were the section exactly median to the cone the seed angles could only appear as wall thickenings. It follows also that other sections more tangential than this would show seed angles even better, although cone outlines and the seed-stem features would lose in completeness. More or less complete embryos are present in various seeds, but in some cases the seeds failed of fertilization or the embryos are not conserved.

PLATE 52. *Cycadeoidea.* Enlarged views of longitudinal and transverse cone sections.

Photograph 1 (to left).—*Cycadeoidea Wielandi* (specific reference doubtful). Yale trunk 131, section 909. ×3. (*Cf.* Volume I, Plate XXII.) Longitudinal section of cone in which the woody cylinder of the peduncle and other features appear with diagrammatic clearness, save that the outer interseminal scale tips and micropylar tubes crumbled away somewhat during the final thinning of the section. But close inspection shows the position of the outer surface, which is marked by a faint line very close to the bract on the left side of the fruit. Inasmuch as the bracts on both sides of the fruit are in this section visible from their insertion on the peduncle throughout quite their entire length, the section must lie in very nearly the true vertical median plane. The hypogynous disk-insertion line is here much smaller than in various other cones of different species, being reduced to a mere basal furrow, which leaves it improbable that the fruit ever bore a disk.

Photograph 2 (to right).—*Cycadeoidea Dartoni* (?). Yale trunk No. 210. ×3. Transverse section through two distinct series of fruits, one mature, the other presumbaly just past the shedding of hypogynous disks. In the case of the upper large fruit the section passes near enough to the base to cut away all that central portion of the convex parenchymatous cushion which bears the fertile-seed stems; only the outer basal zone of sterile scales is visible. In the lower large fruit there appear 3 seeds, the base of a fourth, and some 25 transversely-cut seed stems. The cone thus bore only about 30 seeds since the lowermost seeds appear. A supplementary section passing only 3 mm. lower would cut only stems and scales.

The small size of the bracts of the lesser ovulate series, which has relatively large peduncles, does not militate against the idea that such cones have shed their disks; since the peduncles are of medium size, disk growth and expansion would have been sufficient to thrust aside the surrounding old leaf bases. If the bisexual flowers of two successive seasons be not indicated and the plant was monœcious, a protandrous condition would be indicated; although the suspicion nearly always remains that some form of polygamy or dimorphism might explain the marked variations in cycadeoid flower-buds. The trunk from which this section was cut is very near to *C. Dartoni* type, which has either a dicœcious or more probably a bisexual floral habit. Perhaps the trunks will eventually be found different; but they show well the difficulty of determining the precise kind of sexuality, arising from the fact that any given trunk is only seen in that particular stage of growth reached when the events leading to fossilization began. Doubtless a sure pronouncement can be made when the species in hand with their cotypes can be determined with final accuracy.

PLATE 53. *Cycadeoidea, Lagenostoma,* and *Physostoma* seeds compared. (*Cf.* succeeding plate.)

Photographs 1, 2.—Transverse sections through the seed cone of *Cycadeoidea Dartoni,* showing seeds cut at varying levels from near the base to near the apex. Each contains a fairly well-conserved dicotyledonous embryo.

Photograph 3.—Medial longitudinal section through seed of *C. Wielandi,* showing complete micropylar tube.

Photographs 4, 5.—Physostoma elegans. Transverse sections through summit of seed, that of photograph 5 passing at the higher level. The *corona* of 10 free bundle-supplied *tentacles* arising from the 10 lateral *ribs* incloses *nucellus* and *megaspore membrane;* the sections pass near the base of the funneliform *sinus,* bounded exteriorly by the free tentacles and interiorly by the *nucellus,* with its extension called the *"lagenostome."* (*Cf.* enlarged views, photographs 7, 8.)

Photograph 6.—Lagenostoma ovoides (*cf.* Plate 54, photograph 1).

Photographs 7, 8.—Physostoma elegans. Enlarged views of two complementary sections passing through heavily ribbed shoulder region of seed (photograph 7) and near base of tentacled apex formed by the testal elements.

Note the comparative size of the *Cycadeoidea* seeds and typical Carboniferous seeds of much-varying structure, like *Lagenostoma* and *Physostoma.* [Photographs 2, 3, and 4 to 6 are each 10 times the natural size, and photographs 1, 7, and 8, 30 times.] (*Cycadeoidea* seeds are for the greater part small, reaching their maximum size in one of the most recent forms, *Amphibennettites Bleicheri,* with a length of 1 cm., or very nearly the size of typical Lagenostomas.)

PLATE 54. Sections of typical "coal-ball" seeds of the English Carboniferous, in part comparable to the seeds of *Cycadeoidea.*

Photograph 1.—Lagenostoma ovoides. ×25. The nucellus incloses a mass of tissue with a more or less crenulated outer border and little indication of shrinking. If the border or outer surface crenulation and absence of shrinking prove to be of frequent recurrence, a pre-embryonal stage, or large protocorm, might be indicated rather than a prothallial tissue. McLean (184) compares this structure with the female gamete of Cycads. The section is somewhat oblique.

Photograph 2.—Trigonocarpus Parkinsoni. ×10. Oblique section traversing the shoulder ribs. The large size and great development of the stony layer, equaling that of a peach, are the interesting features of this ancient seed.

Photographs 3 to 7.—Lagenostoma ovoides. ×10. Photograph 3 shows the transverse section through the seed apex or canopy. Photographs 4 to 7 show the longitudinal and slightly oblique seed sections. In photograph 4 the median plane is traversed and the micropylar tube appears, while even at this low magnification several pollen grains are observed in the pollen-chamber space. There are traces of tissue filling out the megaspore membrane.

Photographs 8, 9.—Conostoma oblongum. ×10. Longitudinal and oblique sections. In these and the preceding sections both nucellus and megaspore membrane are invariably indicated. The dark color or apparent density of the outer testa in these calcified seeds is evidently due to the presence of residual carbon. This plate is introduced for comparison of these old seed forms with the silicified Cycadeoid seeds.

PLATE 55. Synangial features in *Cycadeoidea dacotensis*. Yale trunk 214; section 82. ×12 (below) and ×36 (above).

This transverse section through a strobilus on the level of the ovulate cone apex is one of the earliest cut. A small figure of it was given in 1899 (reference 375, Plate X, photograph 18).

Study of these photographs serves very well to make clear the grouping, attachment, and structure of the synangia, especially on comparison with the section from another flower-bud illustrated on the succeeding plate. It may also be noted that one of the synangia cut in median longitudinal section (best seen in the upper photograph) forms the subject of a camera lucida drawing (figure 82, Volume I).

PLATE 56. *Cycadeoidea dacotensis*. Radial longitudinal section through bisporangiate flower-bud.

This plate is supplementary to Plates XXXV to XXXVII, Volume I, and is added because of the clear manner in which the grouped sporangia are outlined. The sporangia have suffered little shrinking and are in many cases filled choke-full of finely conserved pollen grains. Reference to Plate XXXVI, Volume I, photographs 1 and 2, shows the section to vary slightly from the true radial-longitudinal plane, the synangia-bearing pinnules appearing below, but not above, where only the densely packed and adpressed synangia fill out the entire space between the ascending microsporophyll rachis to the right, and the small portion of the decurved tip at the upper left-hand corner of the field included.

PLATE 57. *Cycadeoidea colossalis (?)*. Bisporangiate flower-bud in relief (photograph 1), and thin section (photographs 2 to 6). All these photographs are 3 times the natural size.

Photograph 1.—Dome-like summit of flower-bud in relief, the inclosing bract husk having been removed in order to show the actual surface of the dome formed by the paired spurs arising from each of the microsporophylls. All of the mass on both sides of the dome is made up of hairy bracts, as may be noted in photographs 4 to 6.

Photograph 2.—Longitudinal thin section (No. 880), beginning at base-line of the preceding photograph. This and the following thin sections are all photographed in transmitted light.

(*a*) Synangium of medium size. Although not very perfectly conserved, the synangia are well enough outlined to show that they are relatively few in number as compared with *C. dacotensis*. Immediately above these synangia the sterile body-tissue of the microsporophyll expands to form the large dome or *canopy*.

(*b*) End of once-decurved microsporophyll. On the opposite side of the central cone the decurved and sharply acuminate tip lies closely appressed to the ovulate cone. The latter apparently owes its somewhat abnormal form to a certain amount of wilting-down which has resulted in a considerable open space between the microsporophyll tips and the outer cone surface.

(*c*) Ovulate zone about 0.5 mm. or less in thickness. This zone is only well indicated in the mid-region of the cone and would in any case be much too young and undeveloped for the outlining of individual cells. The palisading of the ovulate zone appears clearest at a magnification of from 10 to 20 times.

(*d*) Insertion of disk. Note interesting transverse fracture lines in the lower part of the disk on both sides of the cone. These have nothing to do with dehiscence of the disk or of the cone, having merely formed in the process of, or subsequent to, silicification.

Photograph 3.—Transverse section of canopy and surrounding bracts cut from the base of the segment shown in relief in photograph 1. The heavy sterile portions of the individual fronds form a series of V's. These are for the greater part symmetrical, but the lower members in the photograph show some variation from complete symmetry.

Photograph 4.—Transverse section at somewhat lower level than the preceding, and above photograph 5.

Photograph 5.—Transverse section through disk and cone, cut at a slightly higher level than point *d* in photograph 2. Disk and cone are both outlined and the same departure from a symmetrical form observable in photograph 2 is present. Crinkling of the disk is normal, and the general appearance of the central cone suggests an aborted condition. The bracts are often constricted near insertion.

Photograph 6.—Transverse section through bracts of preceding flower-bud and an adjacent leaf base, the bundles of which are figured in the notes on *C. colossalis*.

Observe that it is easy to visualize the form of the microsporophyll components in the present flower-bud. The pinnule development is the only feature not fully revealed by these sections; it is, however, slight. In fact, but a very small degree of reduction, with the shortening of the decurved frond tip, would result in a microsporophyll approximating that of *Ceratozamia*. In actuality the fundamental difference from the latter lies in the sporangial grouping in synangia. Moreover, one may go on to comparisons with the leafy sporophylls of open types of cones like those of *Cycadocarpidium* and especially of the Permian Voltzias. It therefore appears probable that all coniferous and cycad sporophylls are closely related to or actually derived from ancient leafy forms. It is now easy to see how by reduction and appression such could be compacted into the hard and often spiniferous elements of present-day cones. Similarly it is easy to see how in such a course of shortening, broadening, and sclerotization, a remaining pair of sporangia, or a single sporangium may finally come to occupy the ventral position. As the sporophyll shortens the sporangia may

be slowly drawn all the way from the nether to the superior surface. The sporophyll elements here found, the spurs, decurved frond tip, pinnules, and sporangia, even suggest a certain analogy to the ovuliferous scale and subtending bract in the Pinaceæ. This may be a simple megasporophyll, as much so as in *Araucaria*.

PLATE 58. Frond features of *Cycadeoidea dacotensis* (*?*) and *Cycadeoidea ingens*.

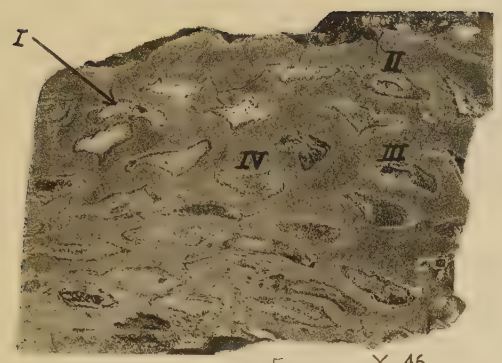
Photograph 1.—Surface of an armor fragment showing form of old leaf bases and scars with the eroded and also the polished transverse sections of one of several adventitious young fronds. The precise species is not determined, but is probably *C. dacotensis*. (*Cf.* the succeeding photographs 2 to 4.) Natural size.

Photograph 2.—Enlarged view of preceding frond. The features are so distinct that form and structure of every bundle in each and every one of the transversely eroded pinnules can be observed. With the aid of photomicrographs 3 and 4, histologic features appear.

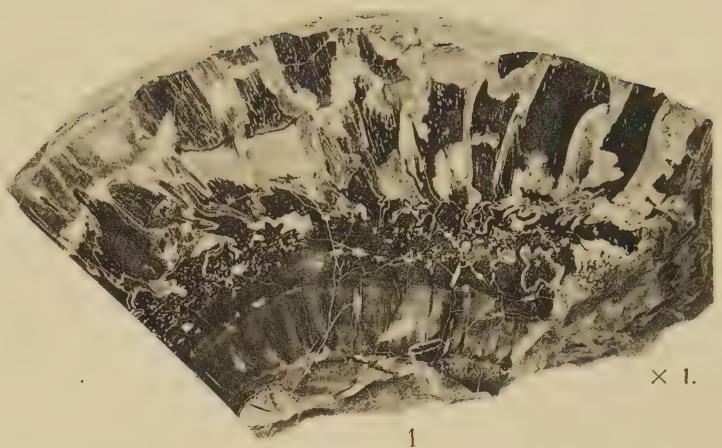
Photograph 3.—Enlarged view of the mid-region of one of the pinnules of the two preceding photographs. ×60. Compare this photograph with the photographic drawing (Figure 45, Volume I). It will at once be noted that the pinnule-bundle structure is essentially the same within close-set generic limits; but specific differences are likewise apparent. In the present form the hypodermal sclerenchyma is uniformly one cell thick instead of several cells in thickness, and the palisade parenchyma is more compact and uniform. Other features vary but little.

Photograph 4.—Supplementary to photograph 3, showing the pinnule ends. (Observe that both photographs 3 and 4 were made directly from the polished surface, and are enlarged 60 times, which sufficiently accounts for the slight lack of clearness.)

Photograph 5.—Transverse section through frond of *Cycadeoidea ingens* (Yale trunk 208. ×3.) Unlike the preceding, this photograph is made from a thin section in transmitted light. The enlargement is scarcely sufficient to show the strongly and uniformly veined under surface of the pinnules indicated by the regularly furrowed lower border. This strong pinnule venation is in sharp contrast to the far smoother surfaces noted in photographs 1 to 4, in which the venation is not directly evident. Probably the pinnule venation only becomes pronounced after the young fronds have reached a considerable size, or the pinnules at least approach the mature size. Hence the presence or absence of a strong venation can scarcely be depended upon as a specific character in such young fronds.

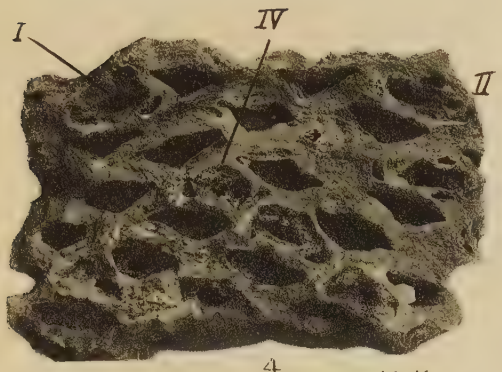


5 × .46.

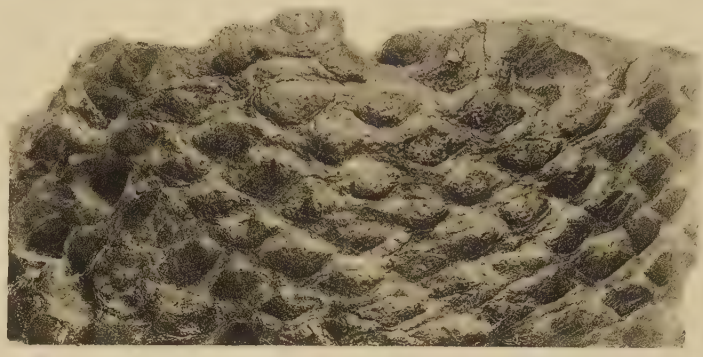


× 1.

1



4 × .46.

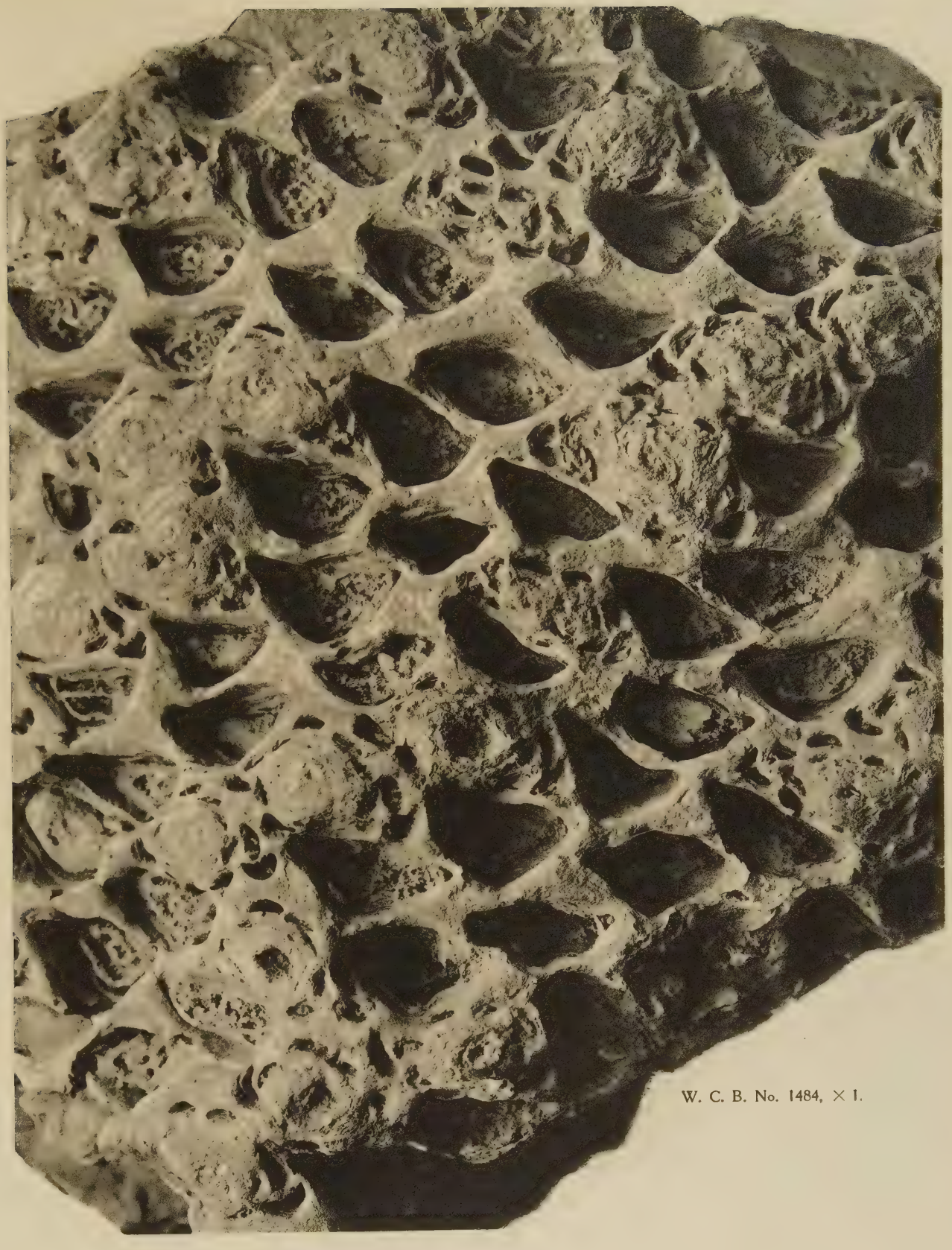


2 × 1.

3

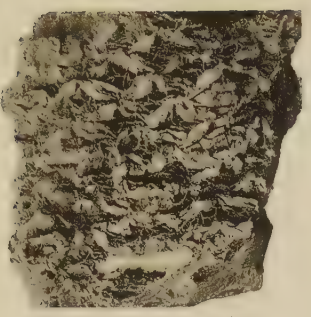
Y. S. 729, × .46.

1, 2, Cycadeoidea mirabilis Lesquereux; 3-5, Cycadeoidea marylandica (Fontaine).

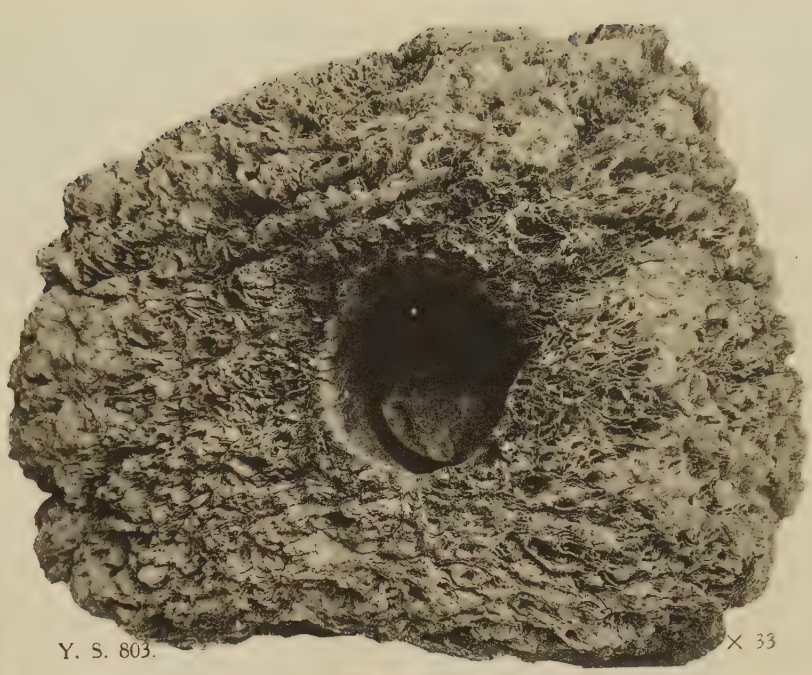


W. C. B. No. 1484, × 1.

Cycadeoidea Bibbinsi Ward (= C. marylandica).



3 × .4.



Y. S. 803. × 33

4

× .4.

2

1

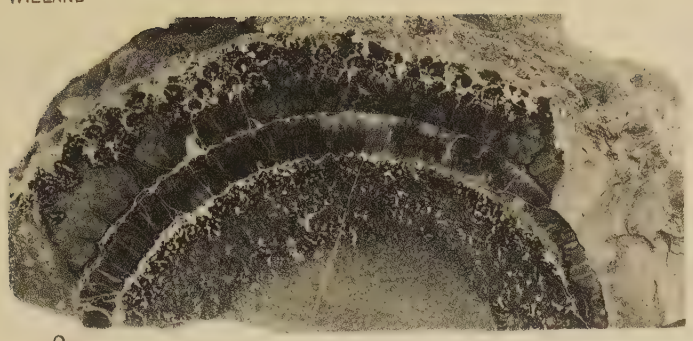
Y. S. 805, × .4.

5

Y. S. 801, × .35.

1-3, Cycadeoidea Uddeni sp. nov., from Upson Shale of Texas; 4, 5, Cycadeoidea microphylla, Isle of Portland.

Typical Series of Piedmont-Black Hawk Cycadeoideas. ×0.09.



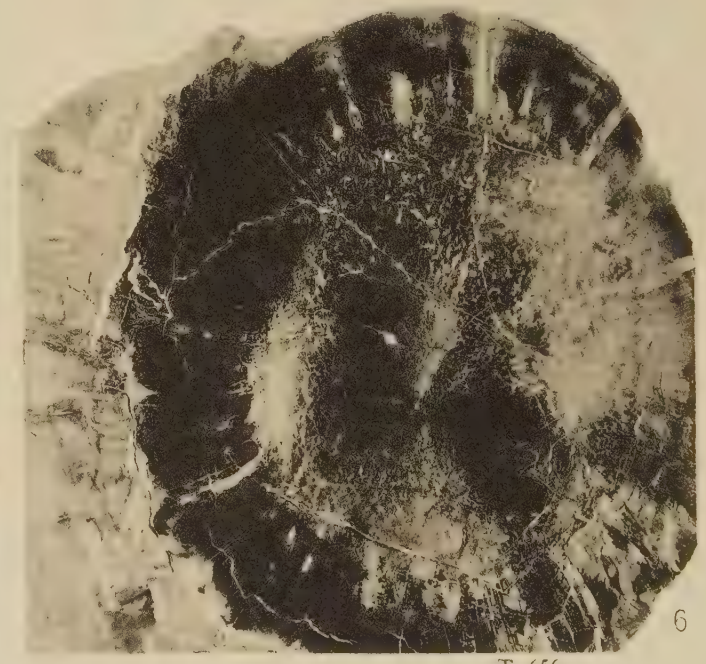
3 T. 630.

T. 630. 4

1 T. 105.

5 T. 656.

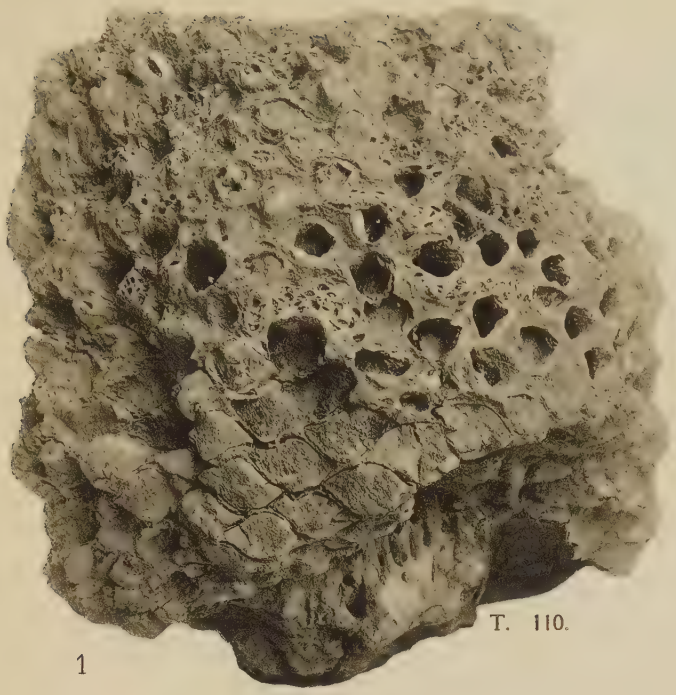
2 T .105.



6 T. 656.

Piedmont-Black Hawk Cycadeoideas.—Continued. .4.

1, 2, C. Stilwelli; 3, 4, C. rhombica; 5, 6, Cycadeoidea sp.

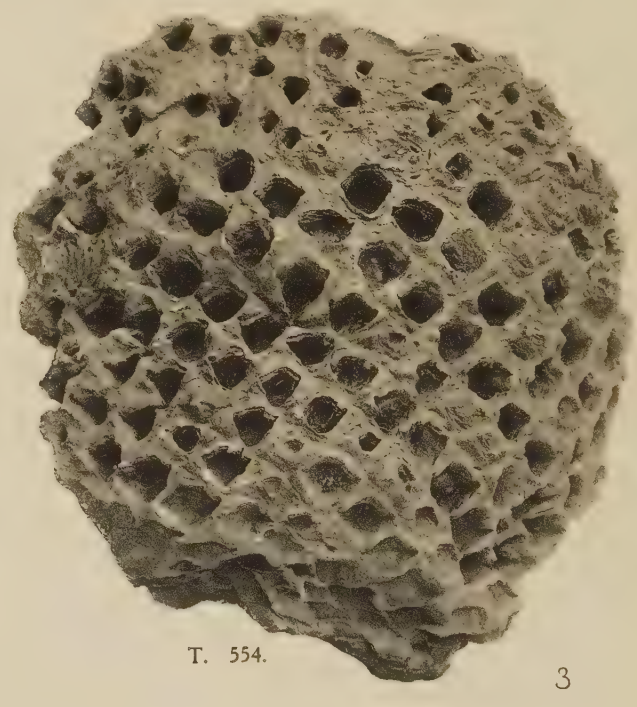

T. 110.

1

T. 642.

4

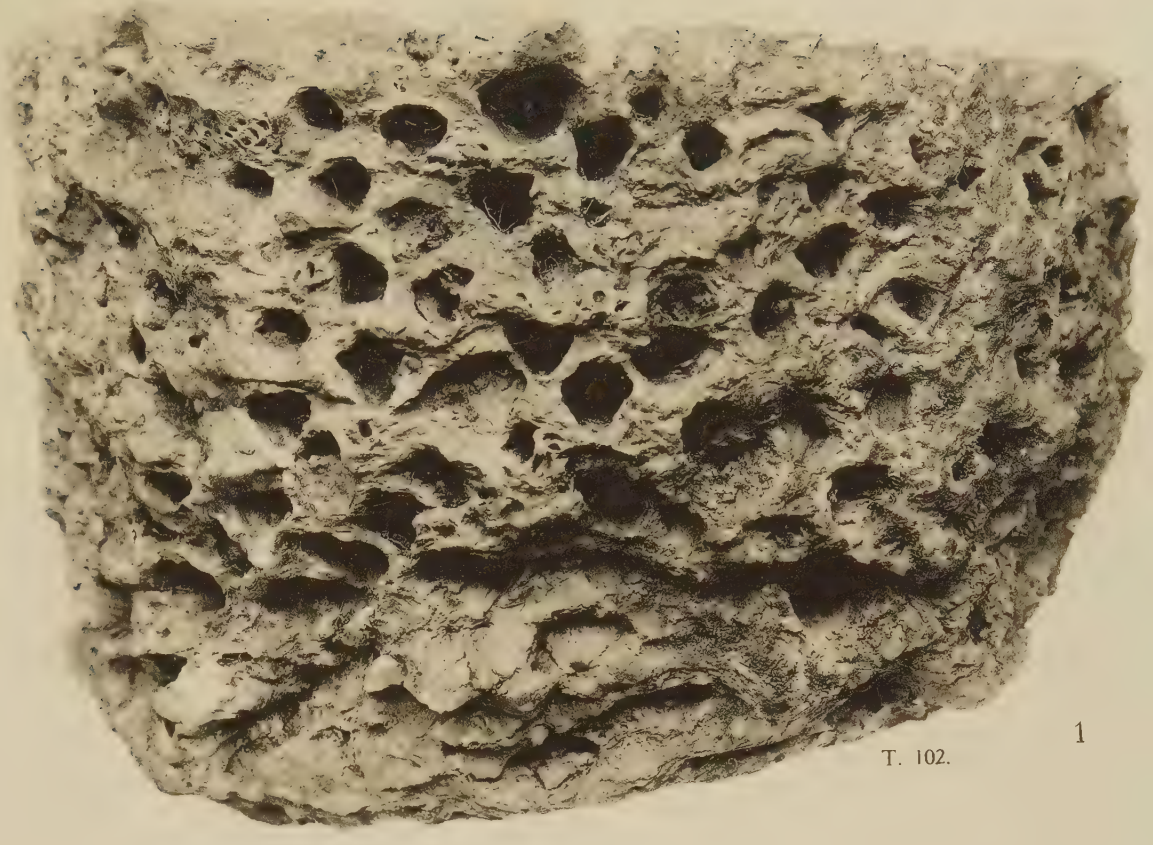
2 T. 115.

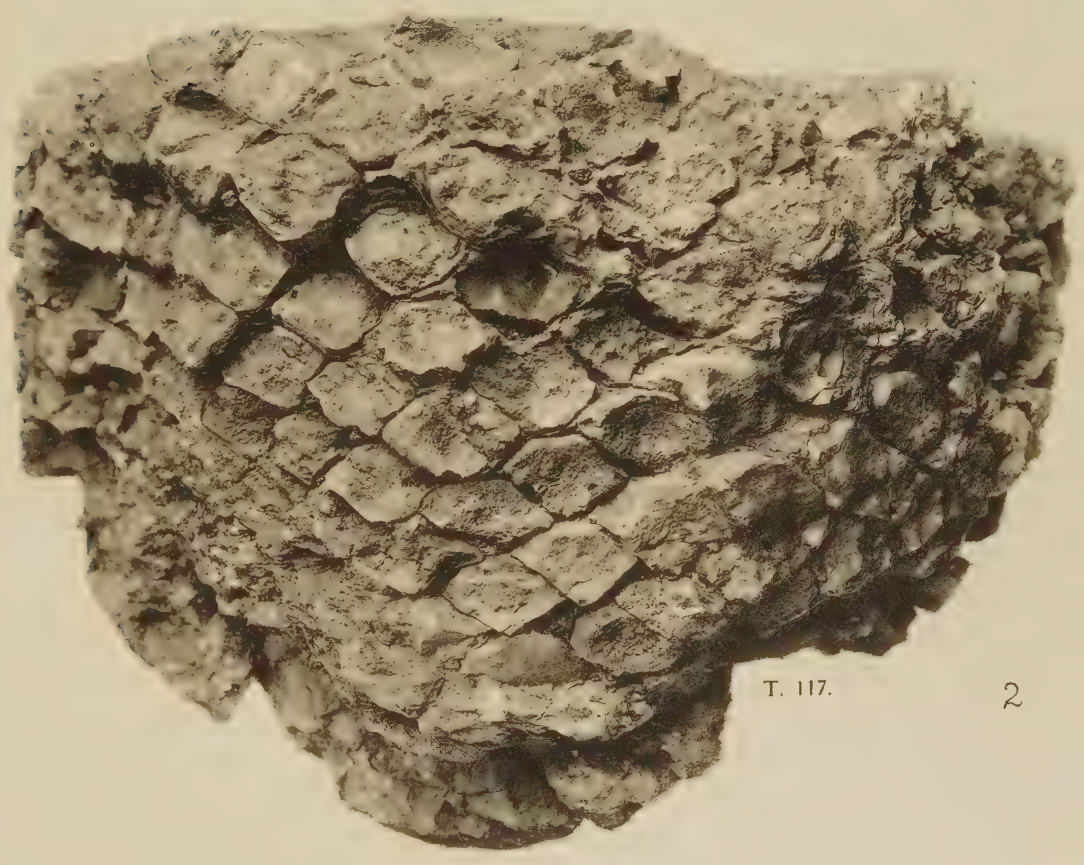

T. 554.

3

Piedmont-Black Hawk Series. Continued. × .25.

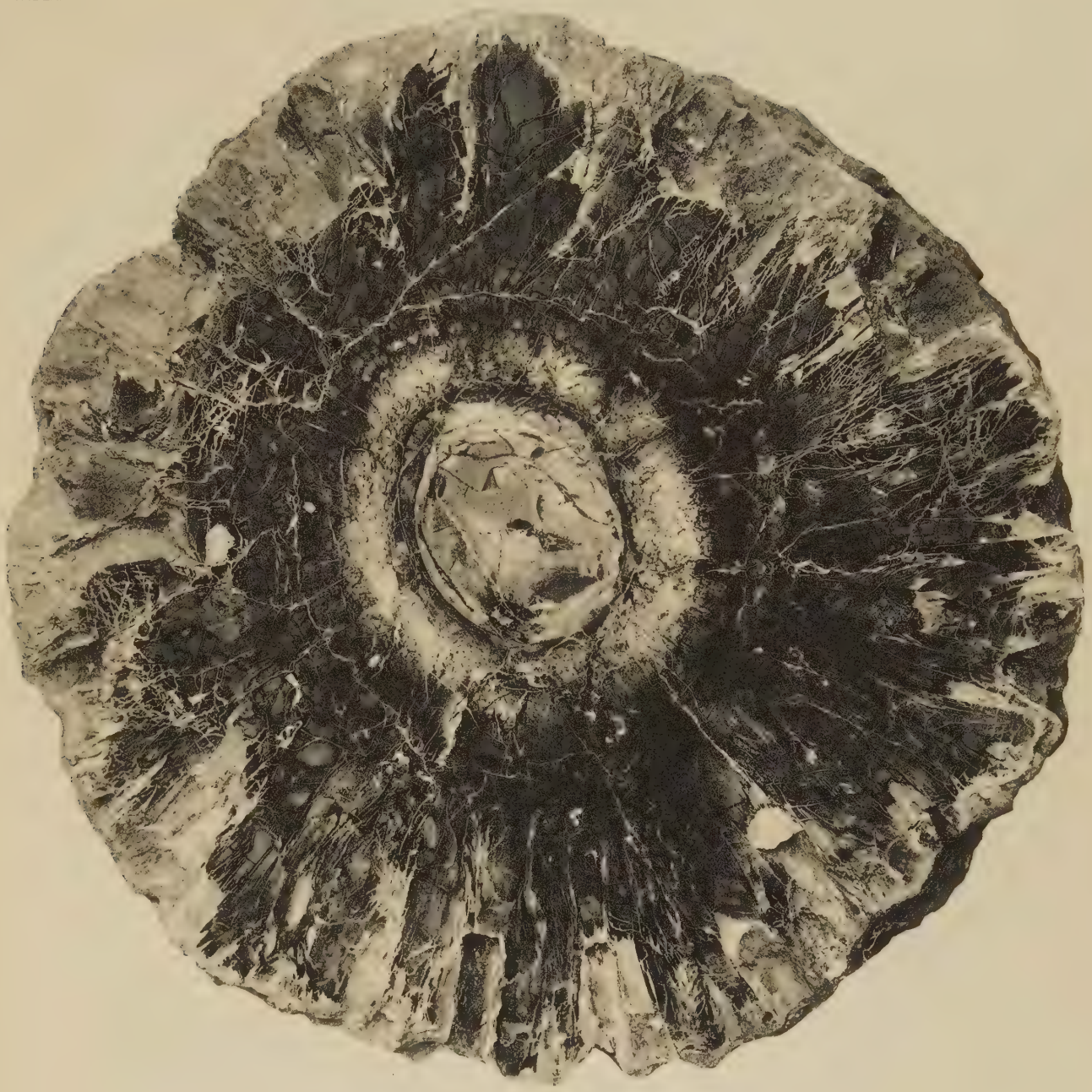
1-3, Cycadeoidea Jenneyana; 4, Cycadeoidea sp.





Piedmont-Black Hawk Series—Continued. ×0.33.

1, Cycadeoidea Jenneyana (cf. Plate 8). 2, C. ingens (cf. Plate 9).



Cycadeoidea Jenneyana. × 0.36.

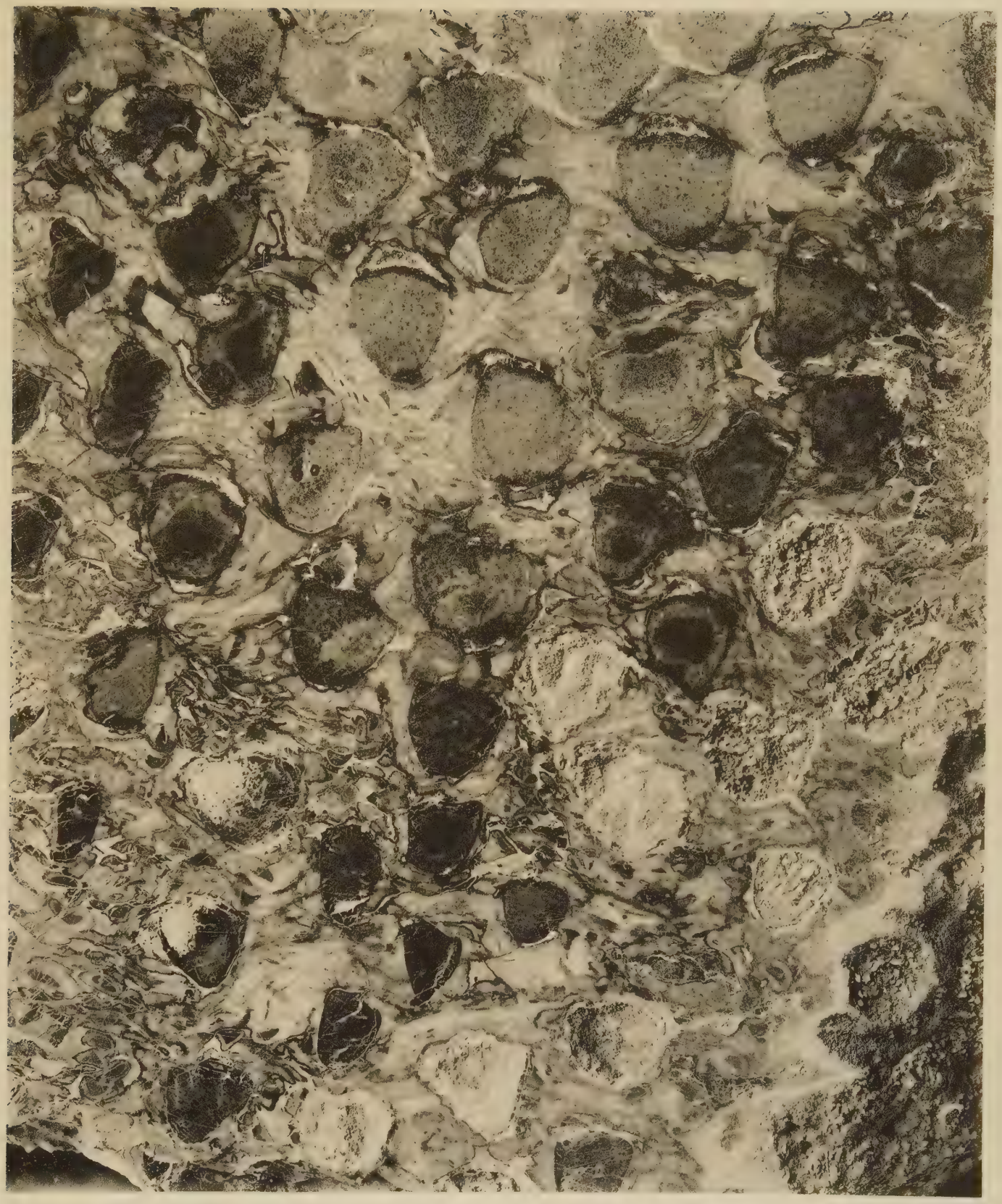
Transverse Section Through Base of Trunk shown in Plate 7, Figure 1. Medulla Light-colored with Large Cone-in-cone Structure, Woody Cylinder Thin, Cortex Narrow, Armor very Heavy and Forming Half the Entire Trunk Diameter.

Cycadeoidea ingens. Y. T. 117. × 0.48

Transverse Section through Trunk Base shown on Plate 7, Figure 2.

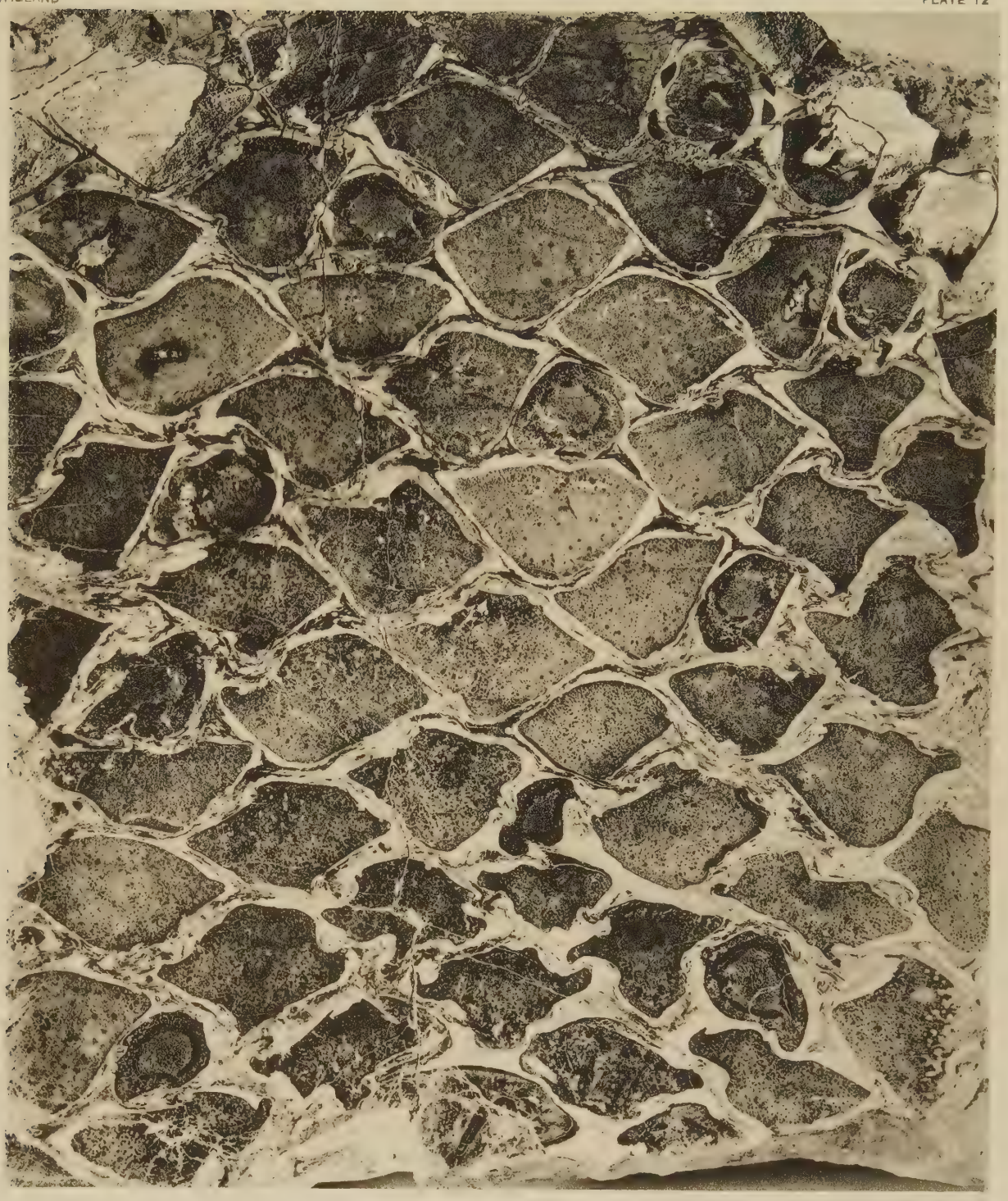
Cycadeoidea Jenneyana. × 1.

Transverse Armor Section of Yale Trunk No. 113, Plate 4. See Basal Continuation on Plate 11.



Cycadeoidea Jenneyana. × 1.

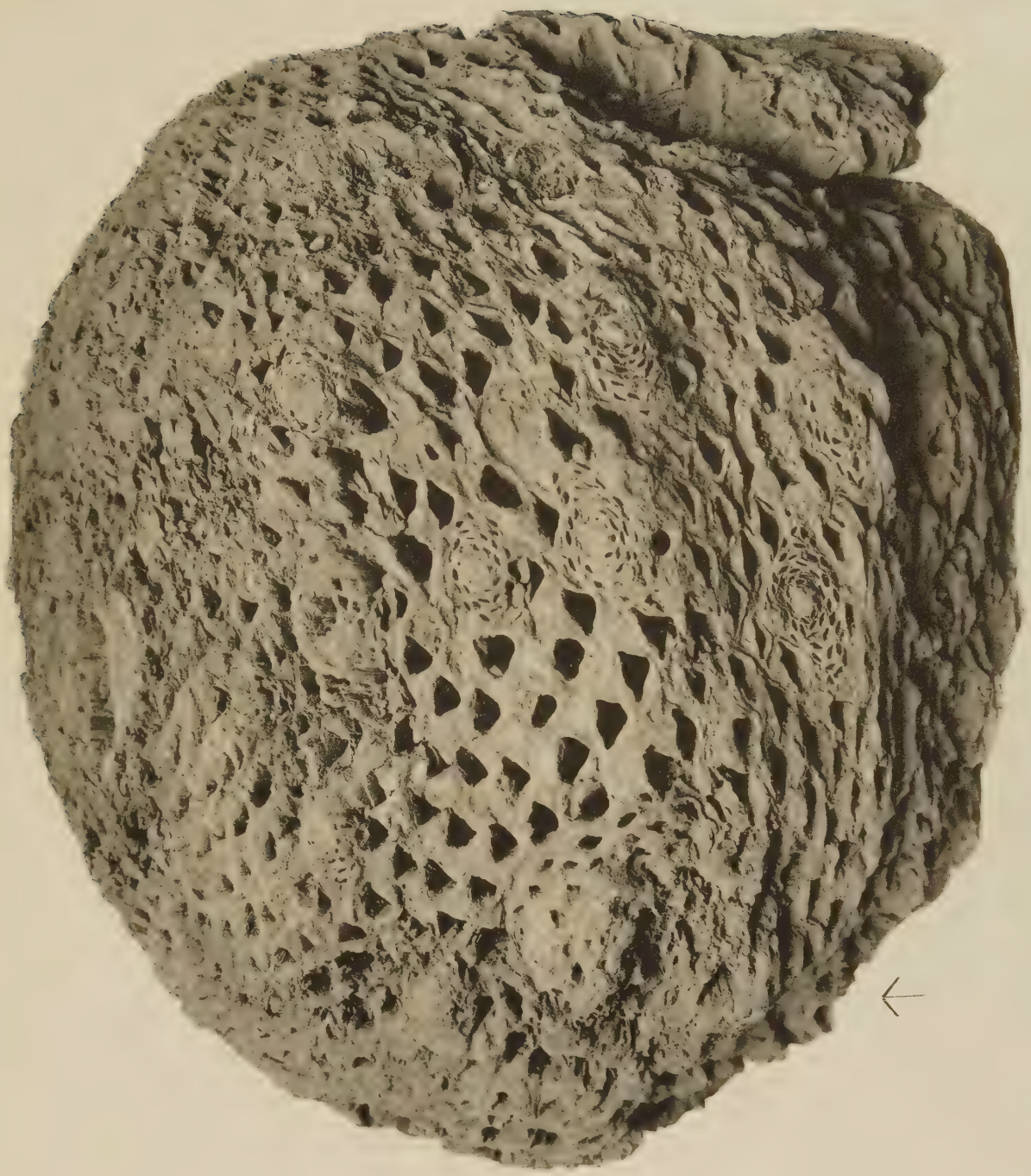
Basal Continuation of Polished Transverse Armor Surface of Plate 10.



Cycadeoidea ingens (?). × 1.

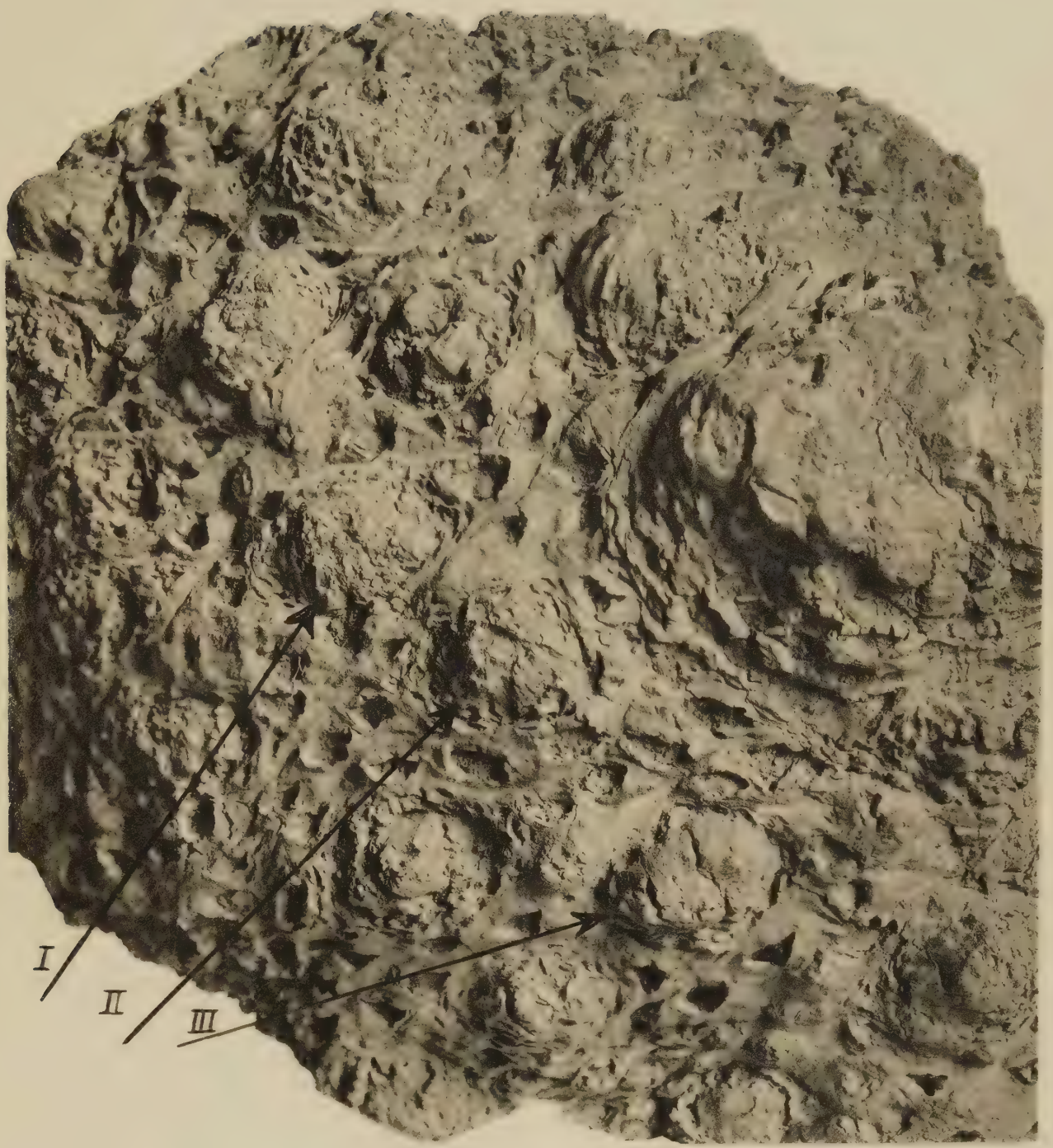
Polished Transverse Section through Armor of Yale Trunk No. 122, Plate 4.

Cycadeoideans from Minnekahta, South Dakota. Collection of the State University of Iowa.

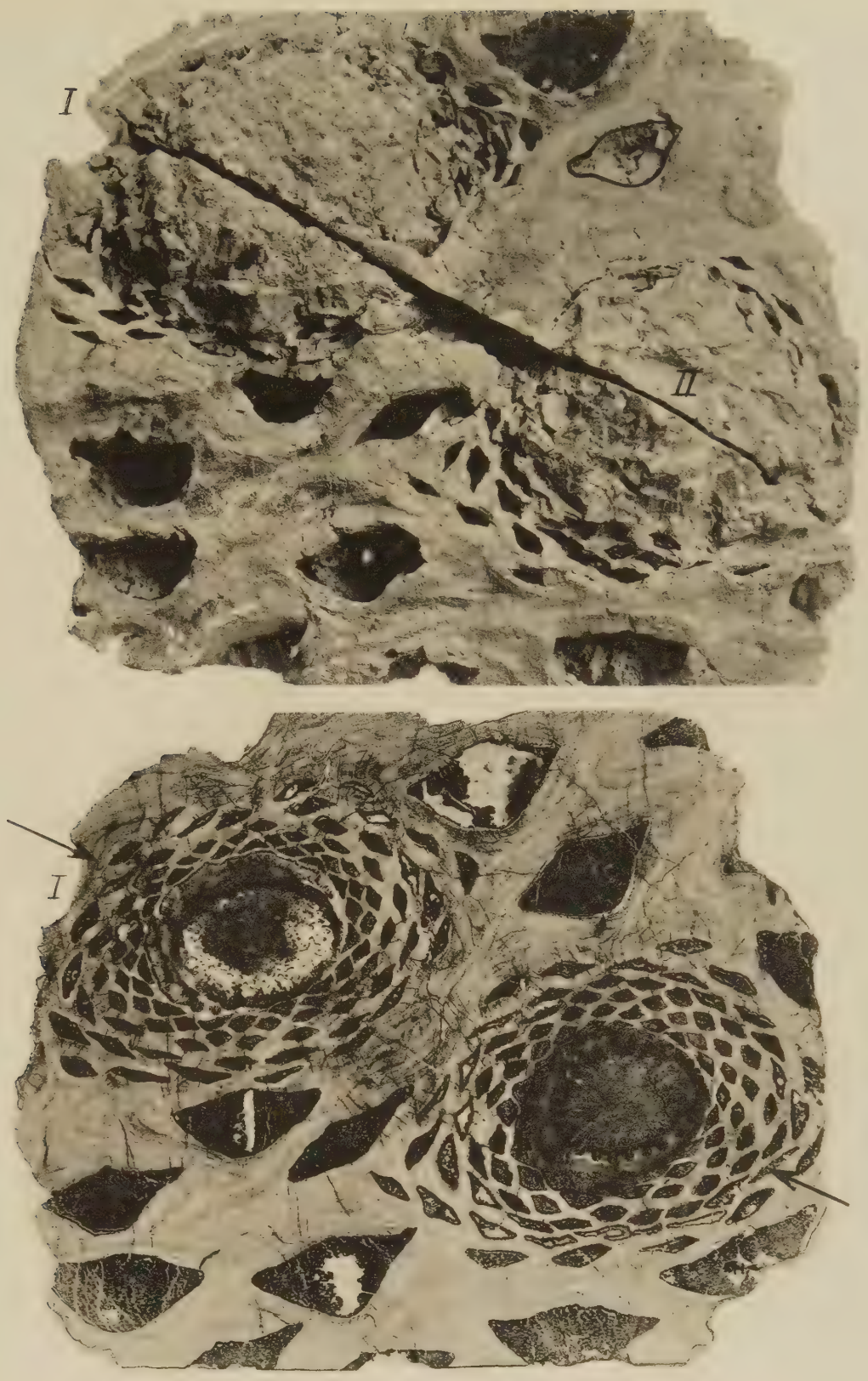


Cycadeoidea colossalis (= C. dacotensis?). Y. T. No. 2. × 0.35
Lateral View of a Minnekahta Trunk with Young Fruits and Branch. Apical View on Plate 15.

Cycadeoidea colossalis (= C. dacotensis?). ×0.35.
Apical View of Yale Trunk No. 2. Lateral View on Plate 14.



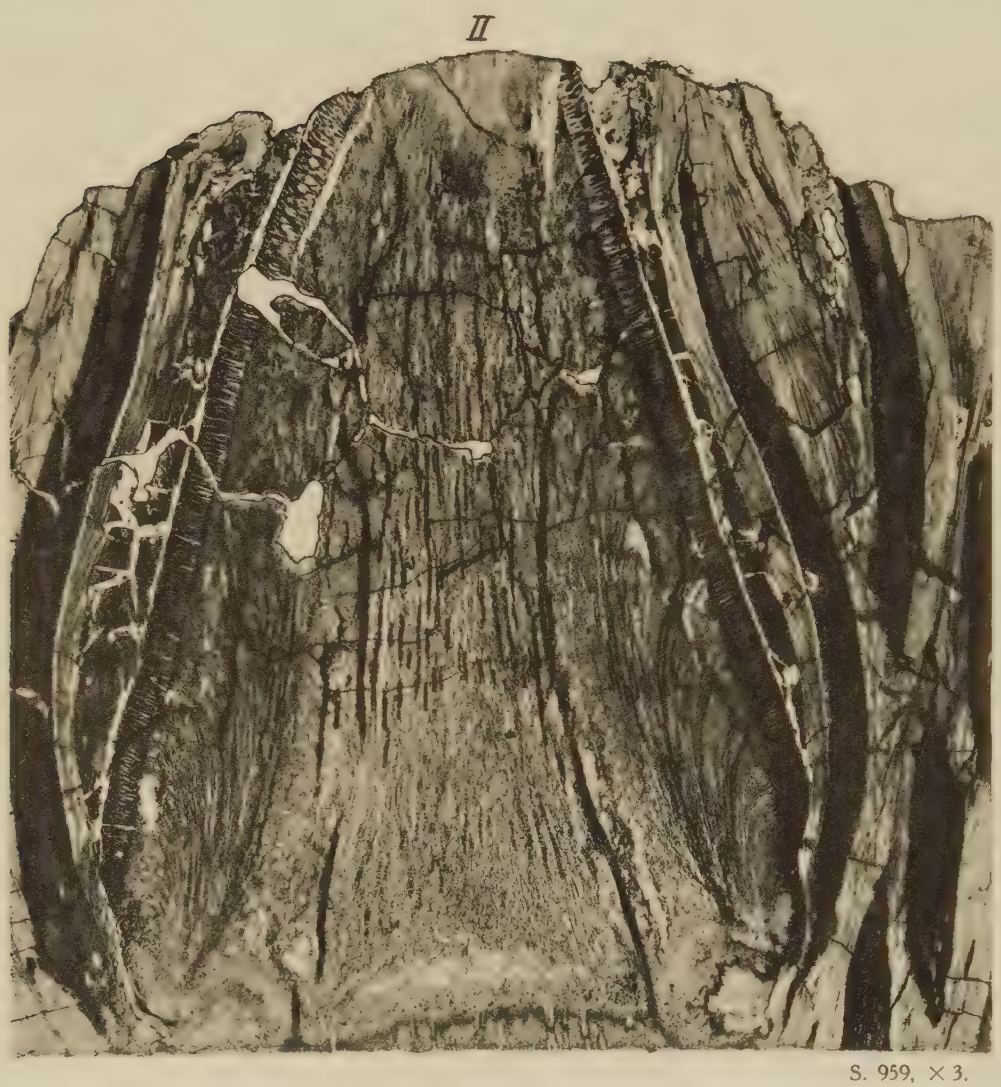
Cycadeoidea dacotensis. Y. T. No. 24, × 0.4.
A Minnekahta Armor Fragment. Fruits marked by Arrows are illustrated on Plates 17 to 20.



Cycadeoidea dacotensis, T. 24.—Continued. ×1.
Surface View and Transverse Section of Peduncles, Axes I, II.

Cycadeoidea dacotensis, T. 24.—Continued.
Transverse Section through Peduncle and Spirally Grouped Bracts of Axis No. II. ×3. (cf. Plate 19.)

S. 959, × 1.



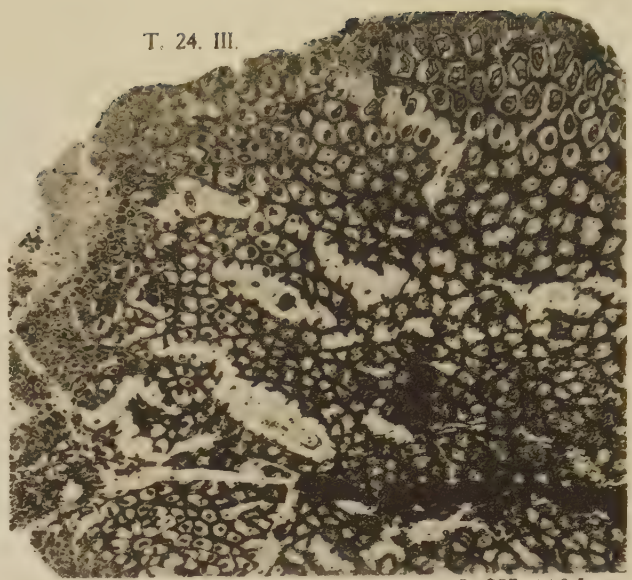
S. 959, × 3.

Cycadeoidea dacotensis, T. 24.—Continued.
Longitudinal Section through Axes I and II.

T. 24. III.

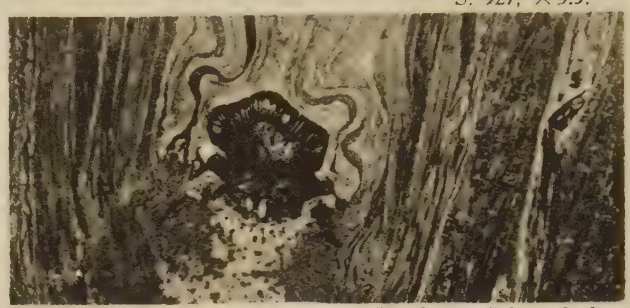
1

T. 24. III, × 1.



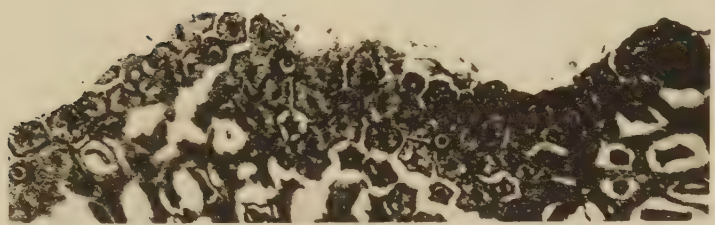
2

S. 927, × 3.5.



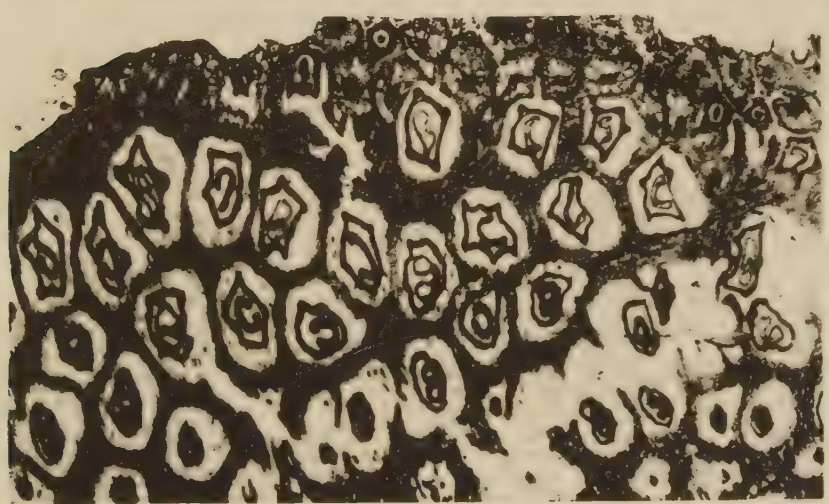
4

T. 393, S. 712, × 2.15.



3a

S. 928, × 10.



3

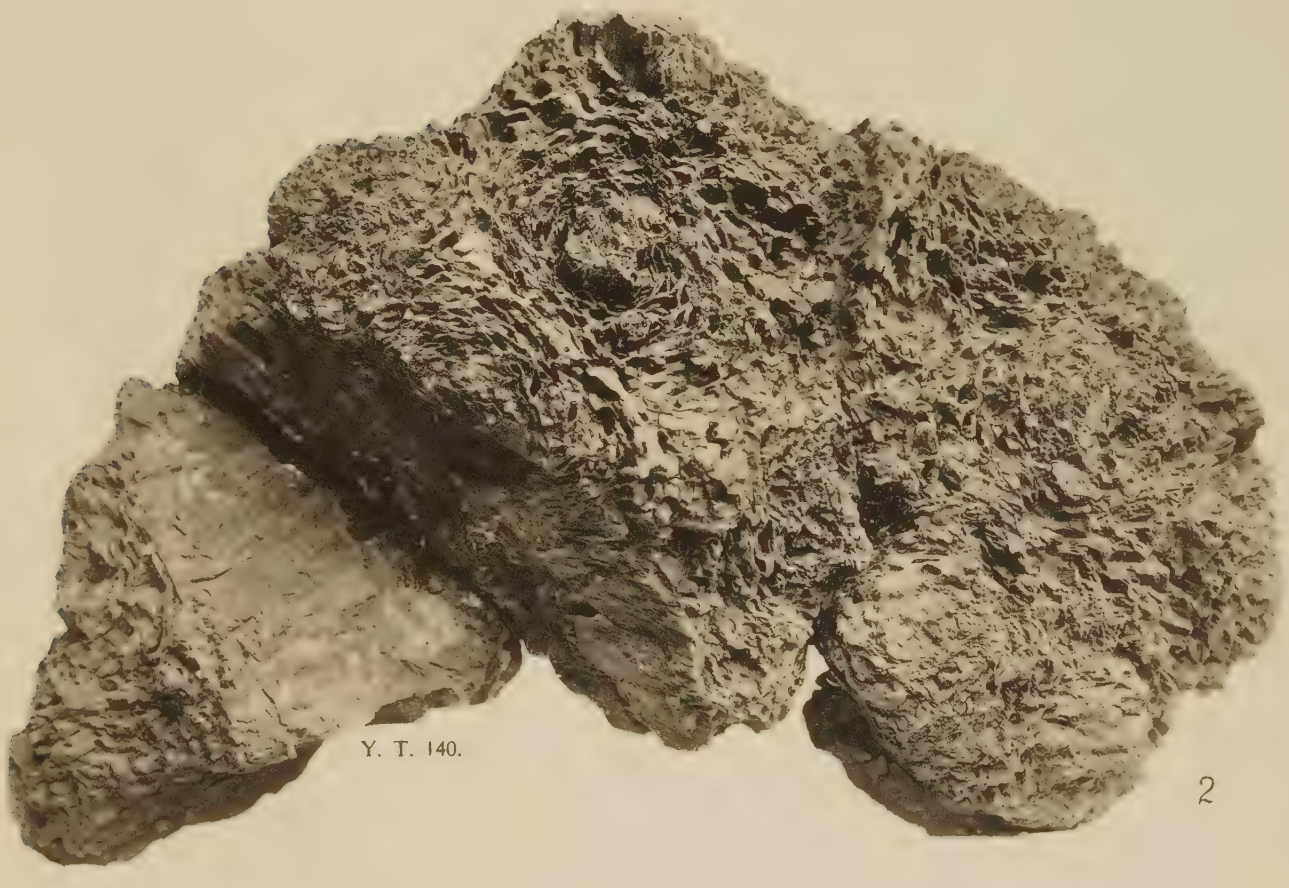
T. 24. S. 927, × 12.

5

T. 131, × 10.

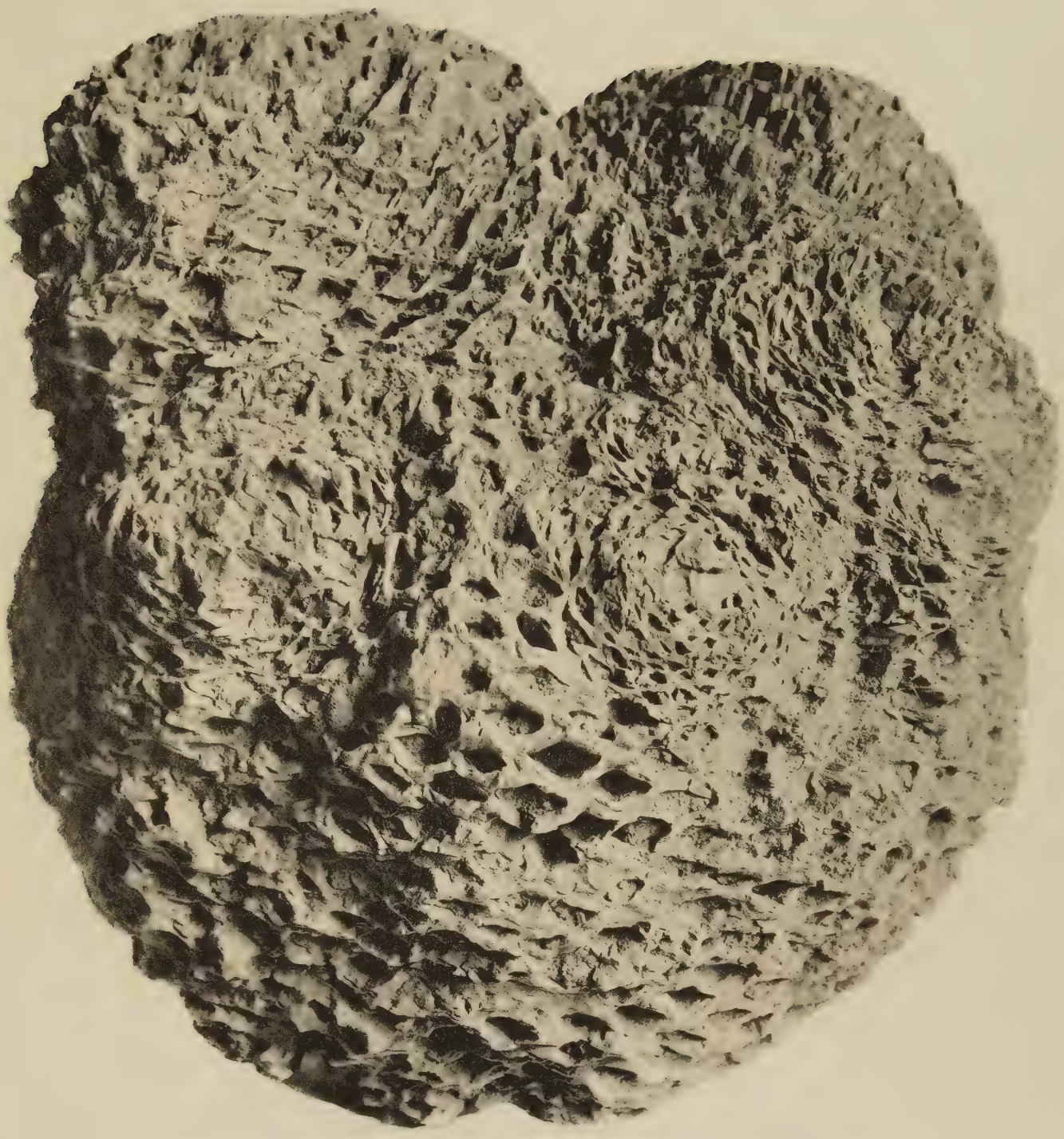
Young and Mature Ovulate Strobili.

1-3a, Cycadeoidea dacotensis (T. 24,—Continued); 4, 5, Cycadeoidea Wielandi (??).



Cycadeoidea (minnekahtensis) marshiana (Wieland emend). × 0.27.

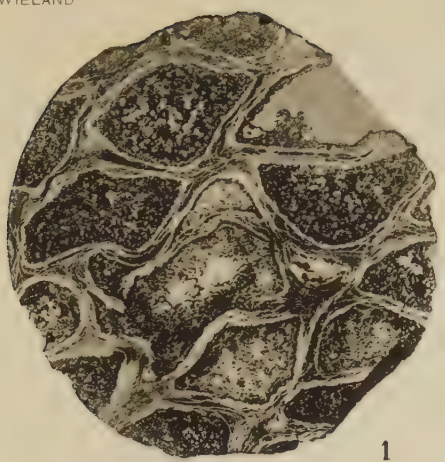
Lateral Views of Juvenile Branched Trunk from Minnekahta.



Cycadeoidea Marshiana. (= C. furcata) ×0.44.
Juvenile Forked Branch from Large Clump, Y. T. 60.

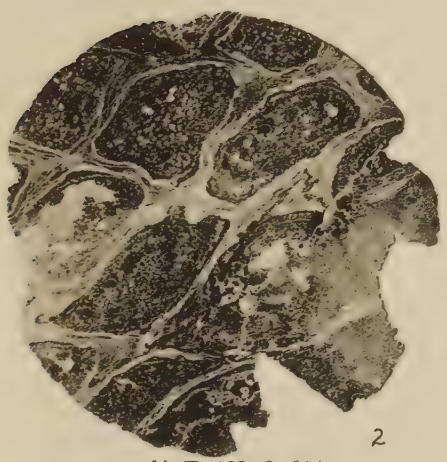
Cycadeoidea Marshiana. Y. T. 129. × 0.33.
Obverse Lateral View on Plate 24, Core Sections on Plate 25.

Cycadeoidea Marshiana, Y. T. 129, × 0.33.
Supplementary to Plates 23 and 25.



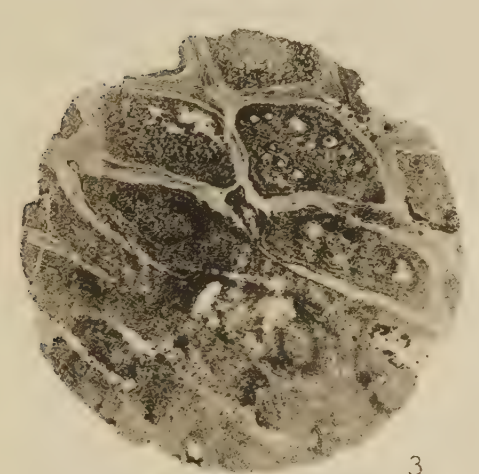
1

Y. T. 129, S. 855.



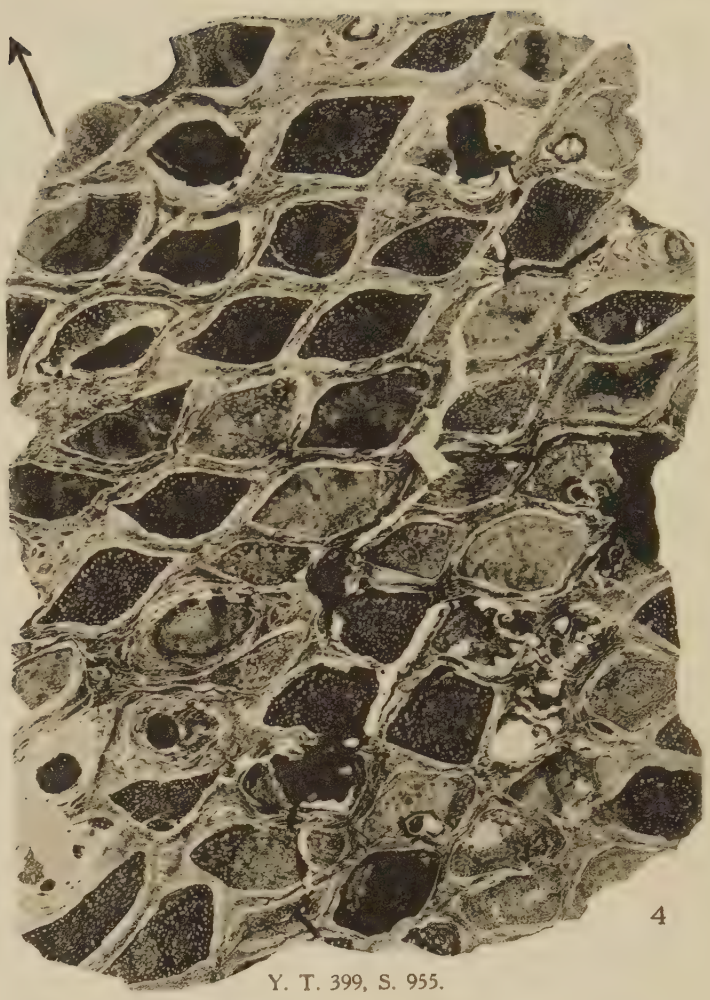
2

Y. T. 129, S. 814.



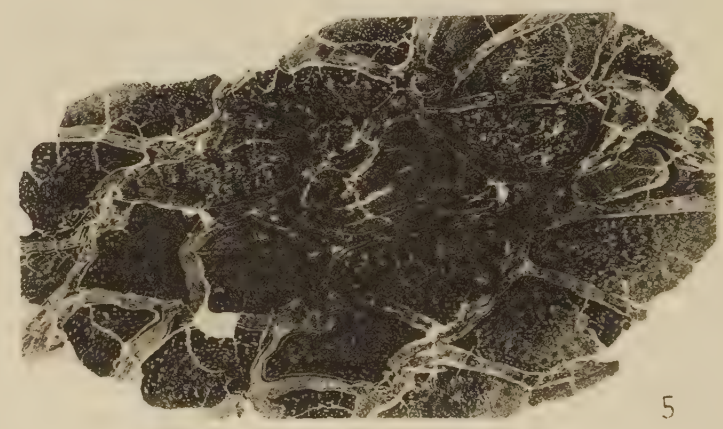
3

Y. T. 129, S. 868.



4

Y. T. 399, S. 955.

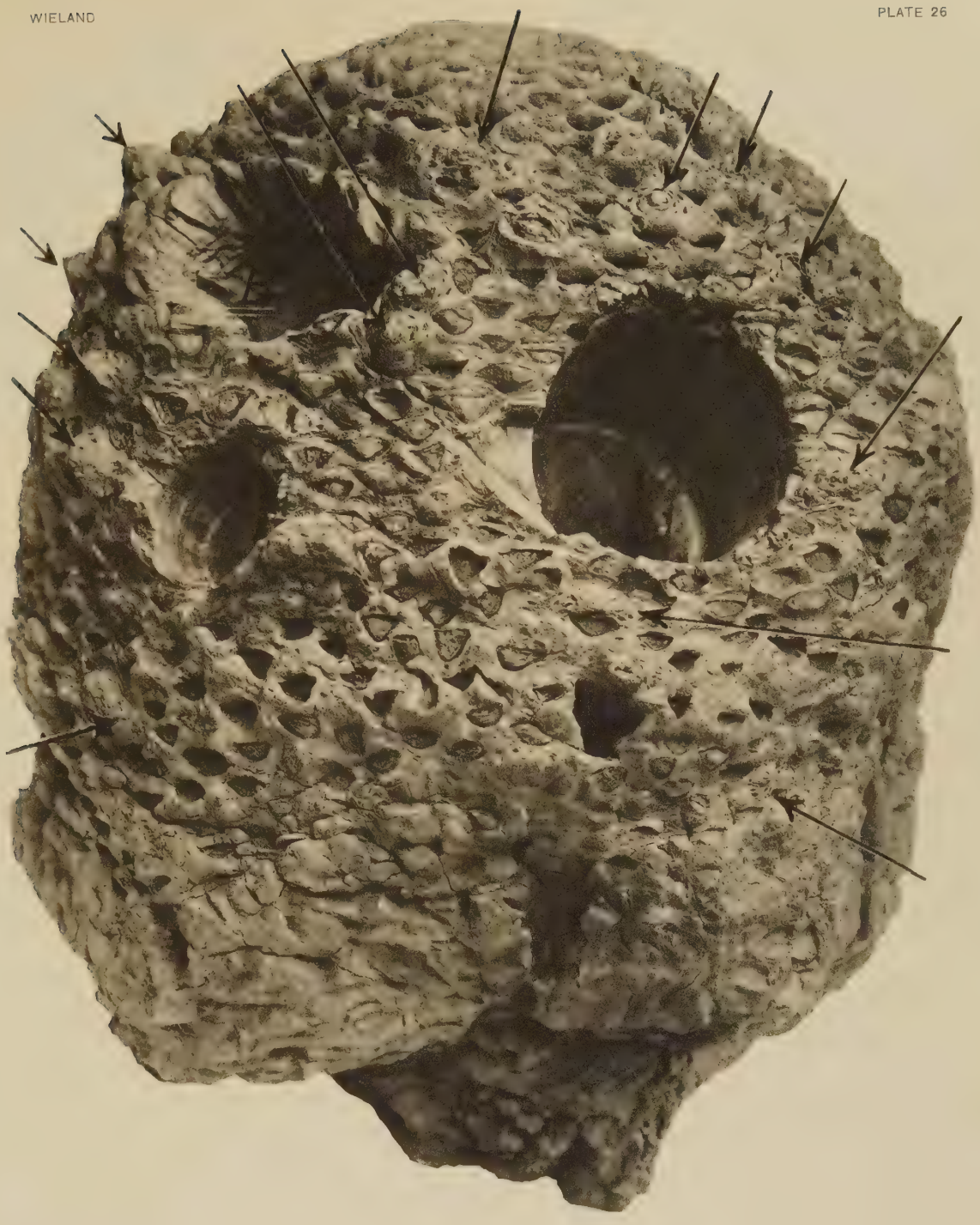


5

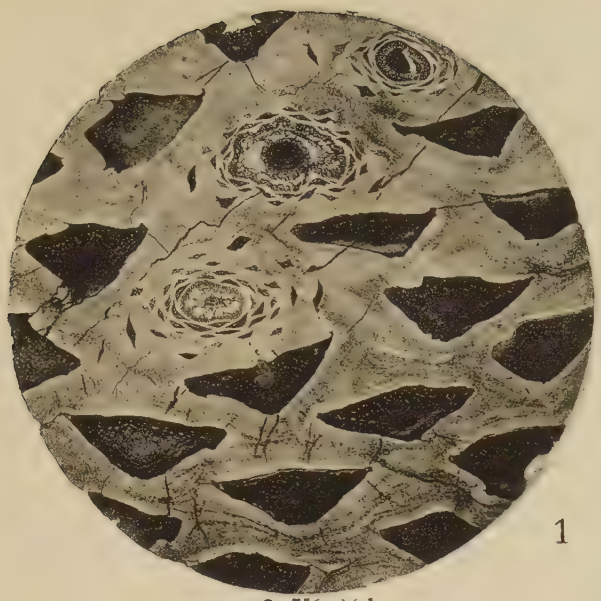
Y. T. 744, S. 890.

Cycadeoidea Marshiana.—Continued. ×1.

Series of Transverse Armor Sections from Yale Trunks 129, 399, and 744.

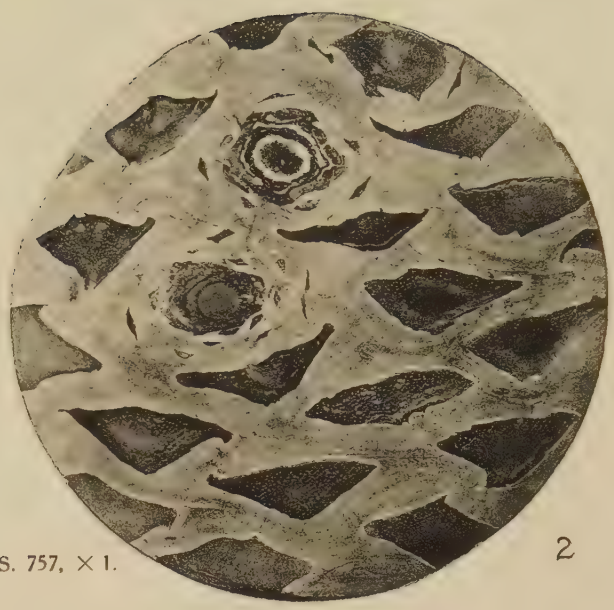


Cycadeoidea Marshiana, Wieland emend, Yale Trunk, No. 3 × 0.43.
Armor Sections illustrated by Text-figures and Plate 27.



1

S. 756, × 1.

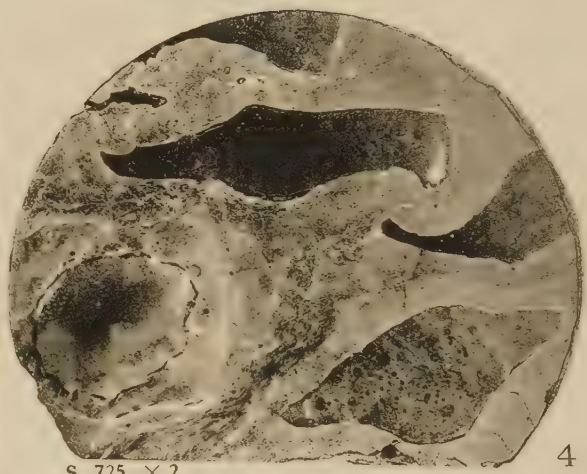


S. 757, × 1.

2

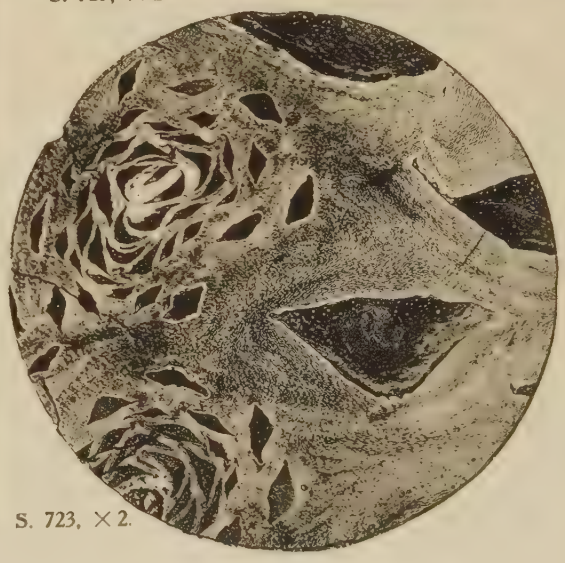
S. 728, × 5.

5



S. 725, × 2.

4

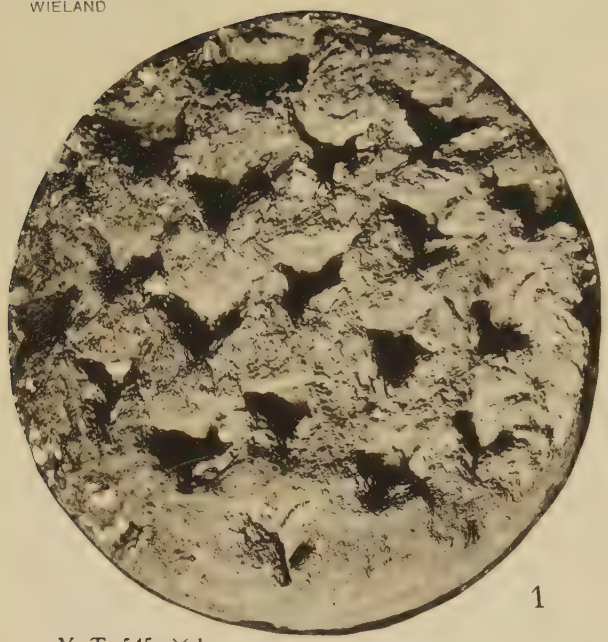


S. 723, × 2.

3

Cycadeoidea Marshiana (Wieland emend).

Cylindrical Core Sections from Yale Trunk No. 3. (See Plate 26.)



1

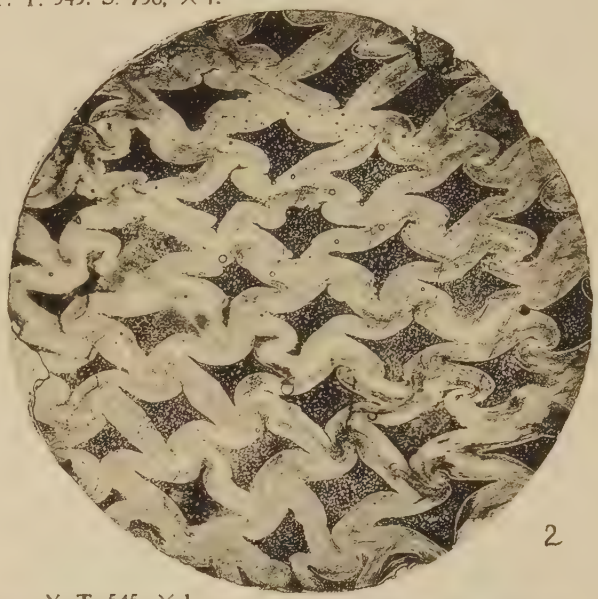
Y. T. 545, × 1.

4

Y. T. 545. S. 758, × 1.

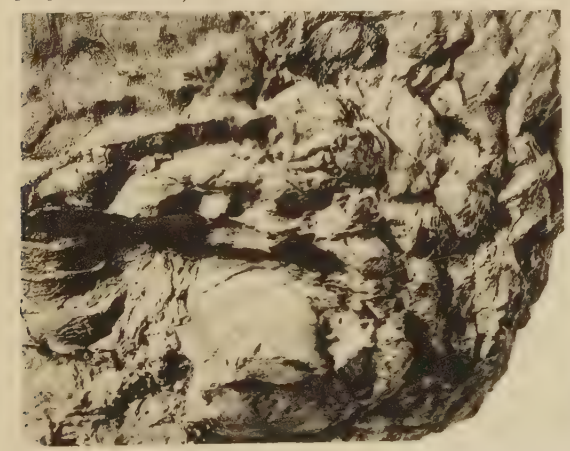
3

Y. T. 545. S. 759, × 1.

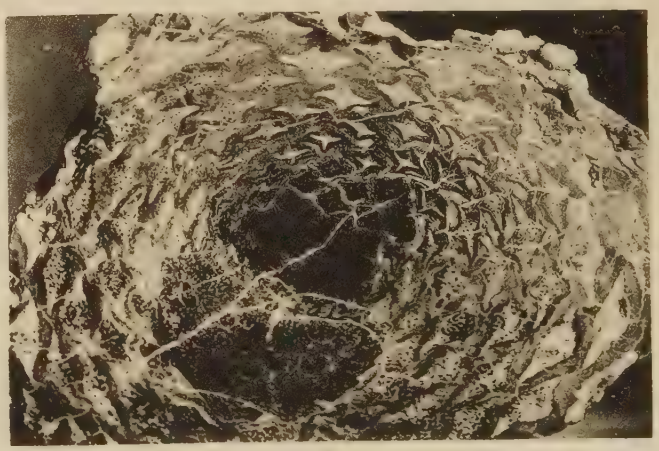


2

Y. T. 545, × 1.



Y. T. 127. 6



5 × 1.

Cycadeoidean Armor Features.—Continued.

1-4, Cycadeoidea pulcherrima; 5, Cycadeoidea (Cycadella) wyomingensis (?); 6, C. (Cycadella) Reedii (type).

1

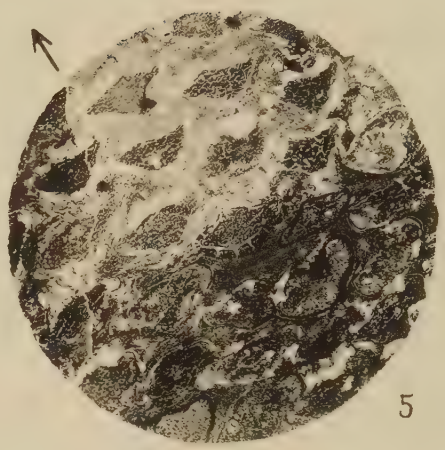
Y. T. 131. S. 965, × 1.

6

Y. T. 800.

2

Y. T. 479. S. 885, × 1.



5

Y. T. 803. S. 849, × 1.

3

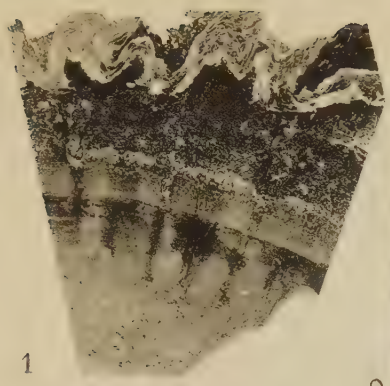
Y. T. 479. S. 879, × 1.

4

Y. T. 479. S. 888, × 1.

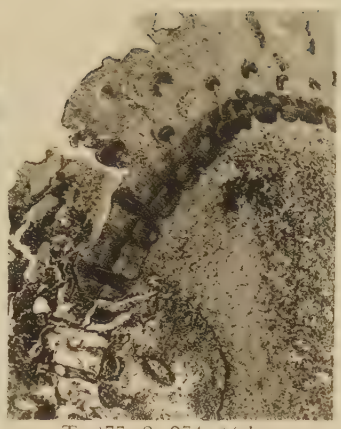
Black Hills and Isle of Portland Cycadeoids.

1, Cycadeoidea cf. Wielandi; 2-4, Cycadeoidea cf. Marshiana; 5, 6, Cycadeoidea microphylla from Portland "Dirt Bed."



1

U. S. N. M. S 981. × 1.

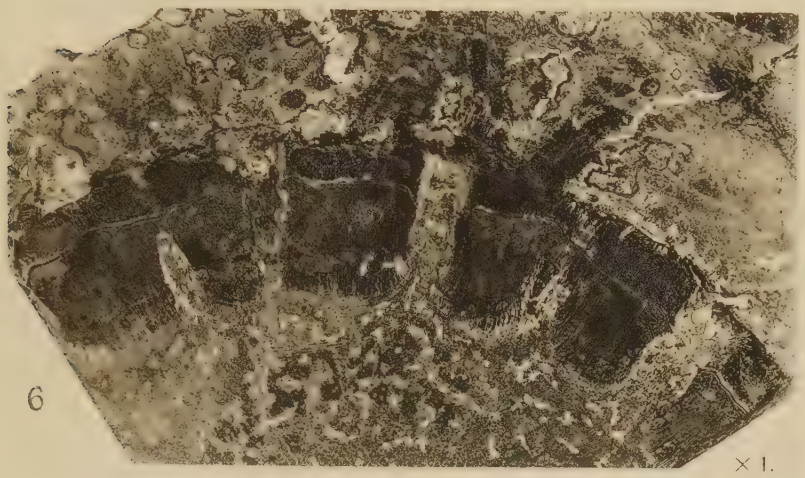


2

T. 377. S. 974. × 1.

3

T. 377. S 972. × 1.



6

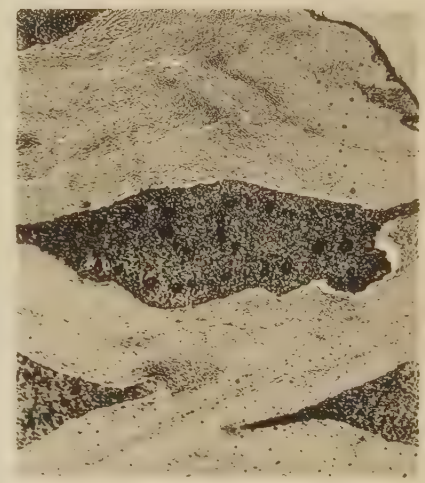
× 1.

4

T. 377. S. 971. × 1.

7

× 3.

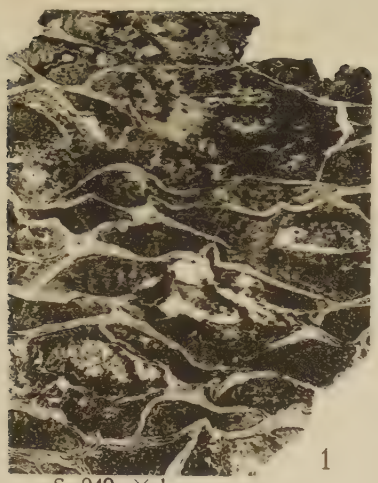


5

× 2.15

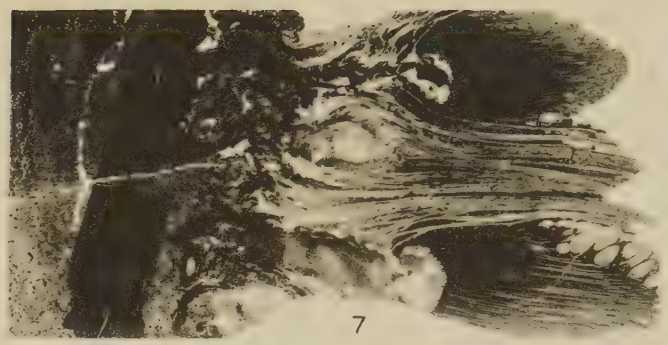
Italian, Isle of Portland, Isle of Wight, and Black Hills Cycadeoideas.

1, Cycadeoidea Paynei or Painei; 2-4, Cycadeoidea sp., cf. nana; 5, Cycadeoidea etrusca; 6, Cycadeoidea megalophylla; 7, Bennettites (=Cycadeoidea) Gibsonianus.



S. 949, × 1.

1



7

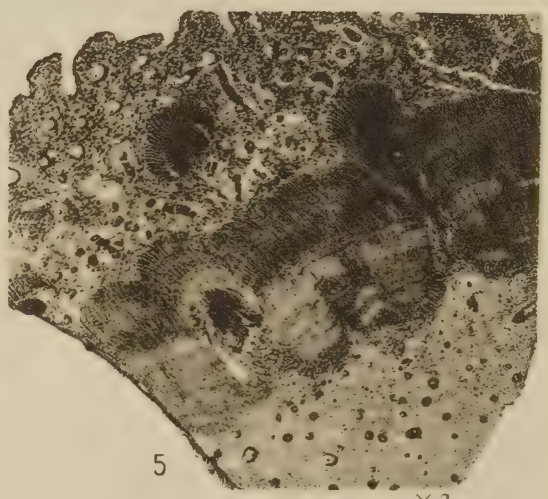
S. 936, × 1.

S. 924, × 1.

2

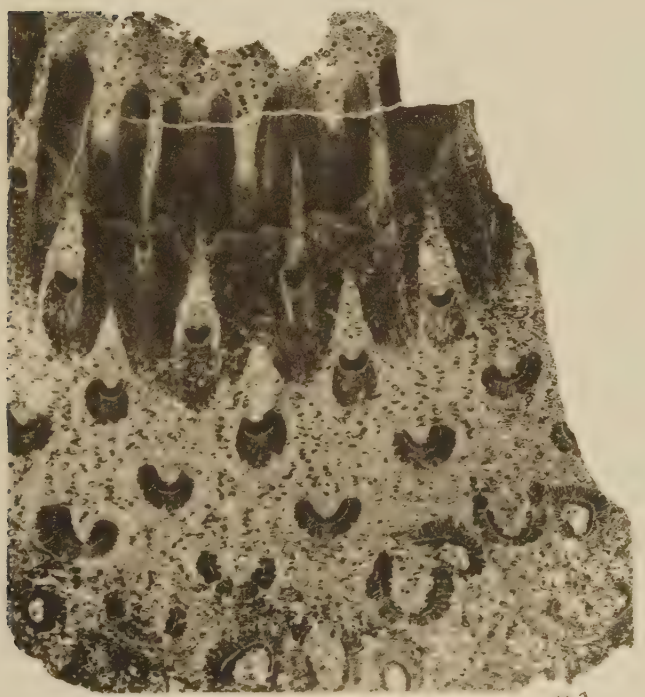
S. 953, × 1.

3



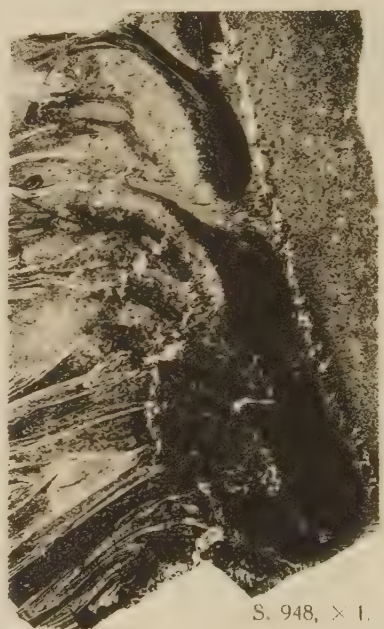
5

× 2.



4

× 2.



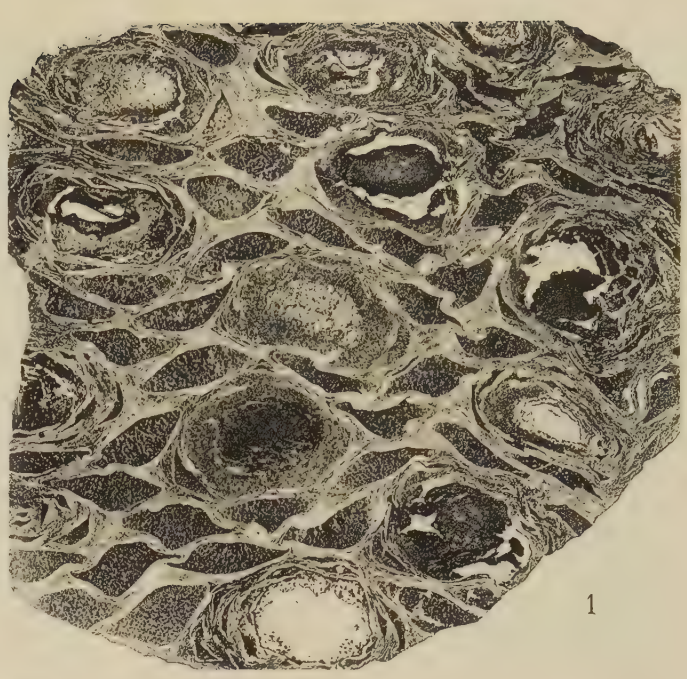
S. 948, × 1.

6

Cycadeoidea Wielandi. Yale Trunk No. 393.

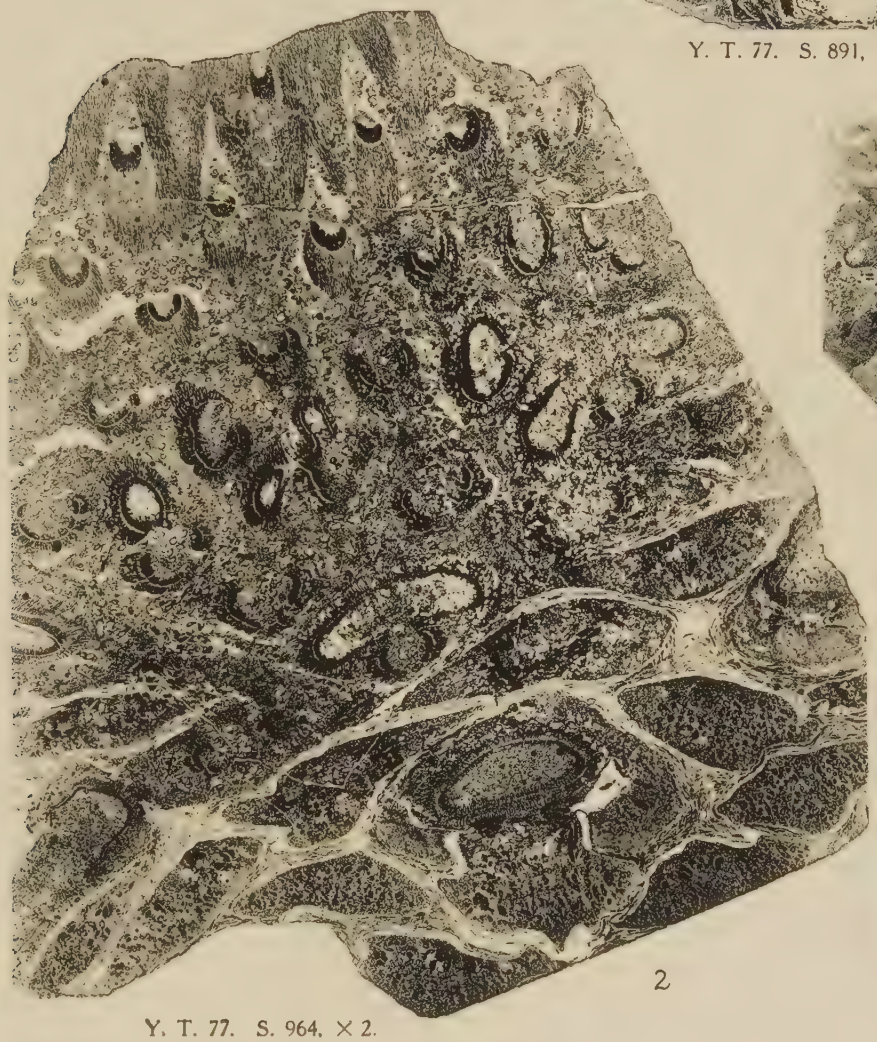
5

Y. T. 744. S. 963, × 1.



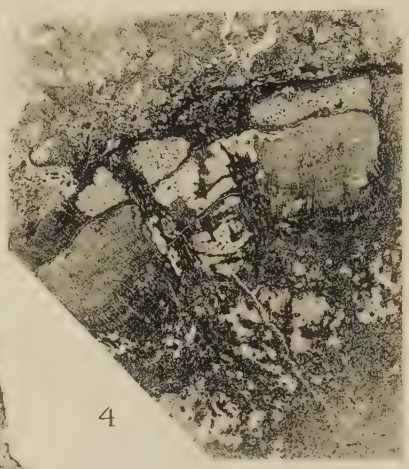
1

Y. T. 77. S. 891, × 1.



2

Y. T. 77. S. 964, × 2.



4

× 1.

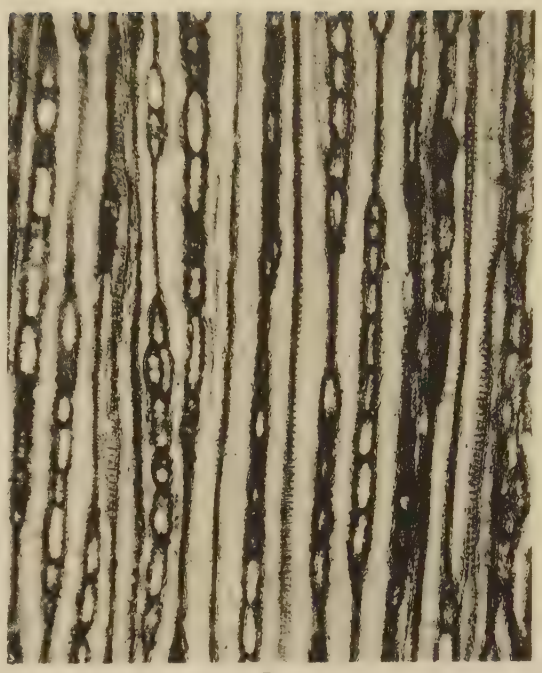
3

T. 393. S. 951, × 1.

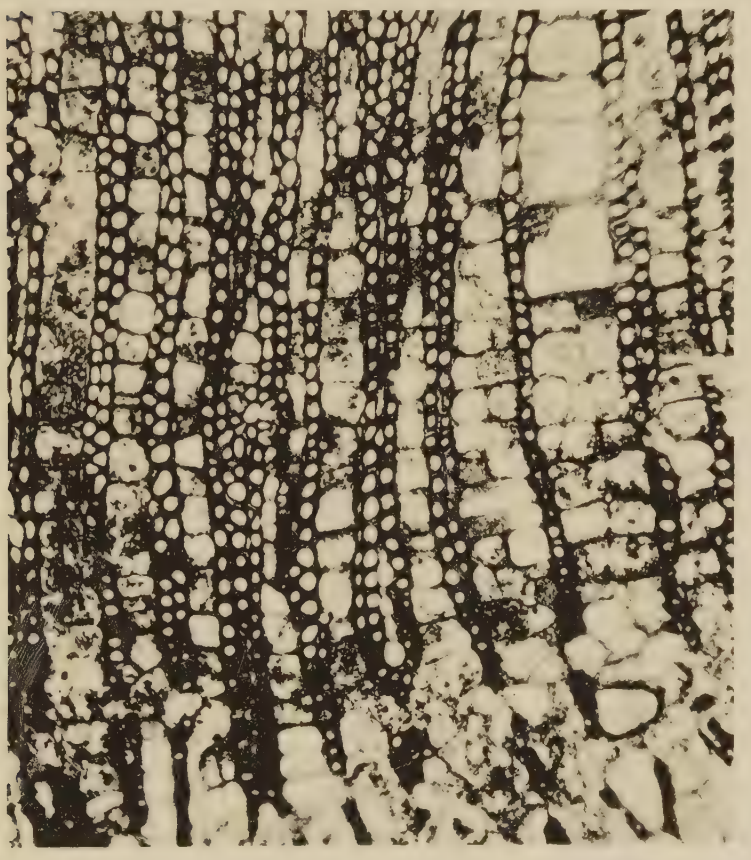
Cycadeoid Cortex and Armor Features.

1-3, Cycadeoidea Wielandi; 4, Cycadeoidea megalophylla; 5, Cycadeoidea superba (?).

1 ×90±.



3 S. 1008. ×100.

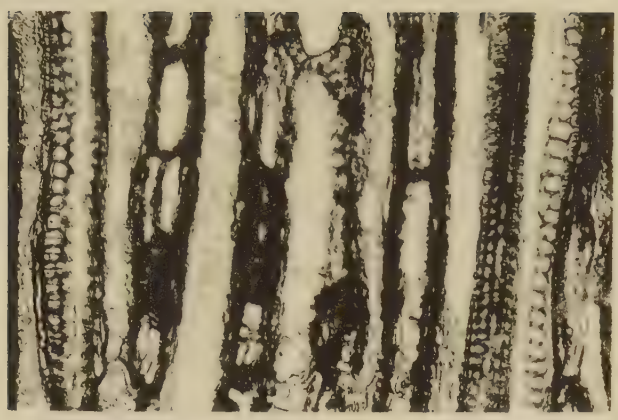


2 ×90±.

4 ×90±.

Cycadeoid Wood Structure.

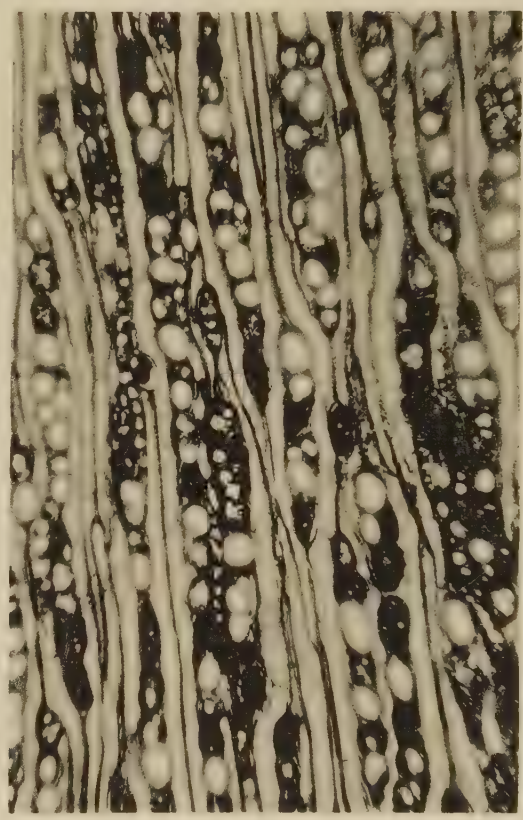
1, 2, Bennettites Gibsonianus; 3, Cycadeoidea Dartoni; 4, Cycadeoidea Paynei.



S. 1008, × 200. 1

S. 1008, × 200. 2

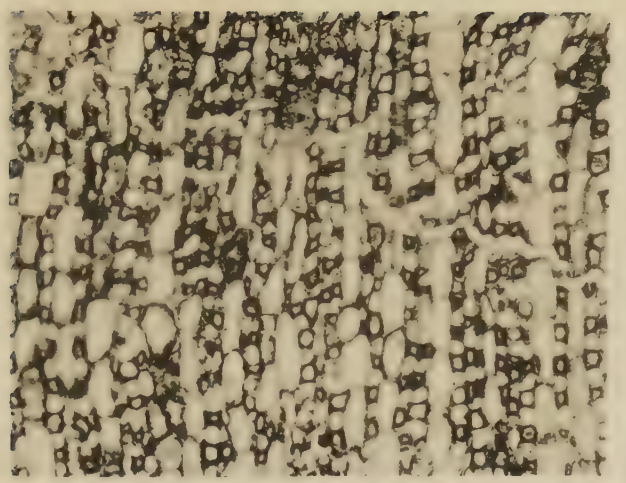
× 190—. 3



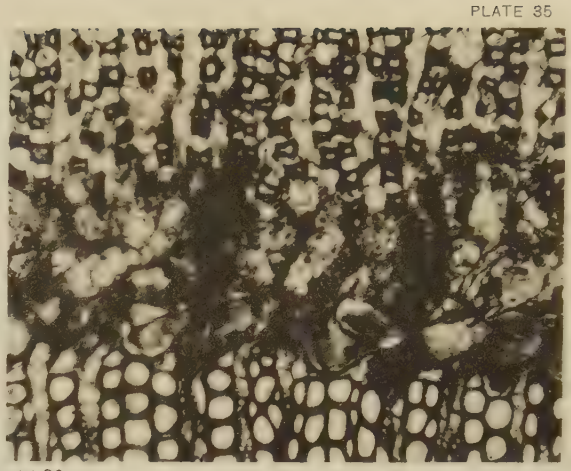
4 × 90.

Cycadeoid Wood Structure—Continued.

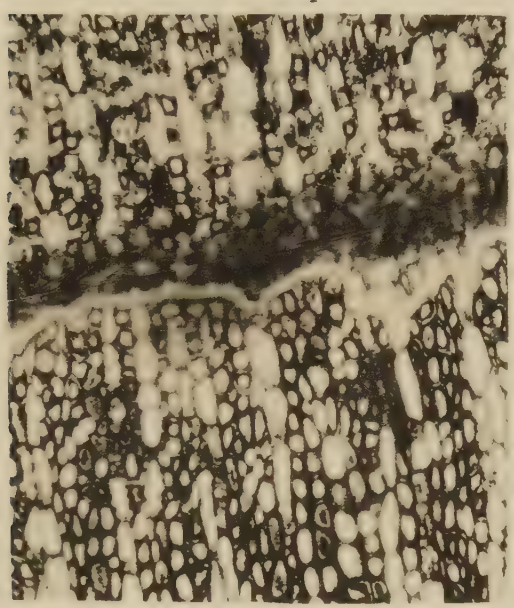
1, 2, Cycadeoidea Dartoni; 3, 4, Cycadeoidea Paynei.



× 90±. 1

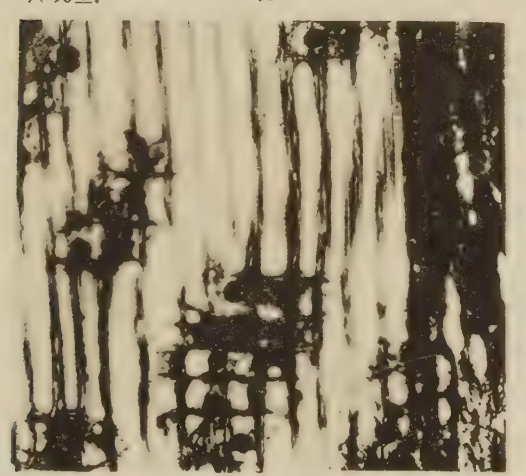


× 90±. 3

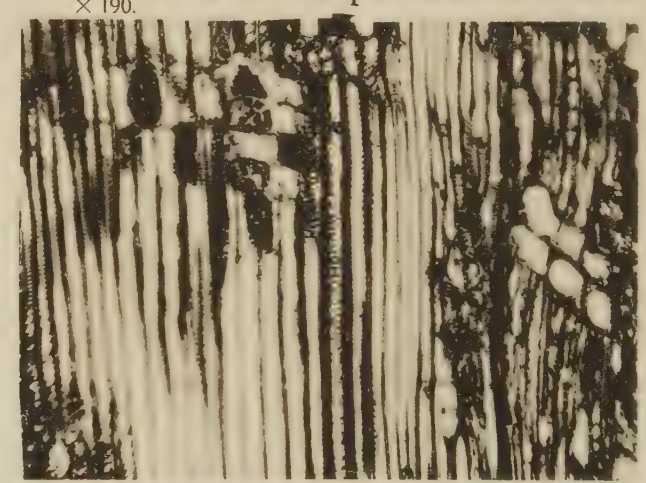


× 90±. 2

× 190. 4



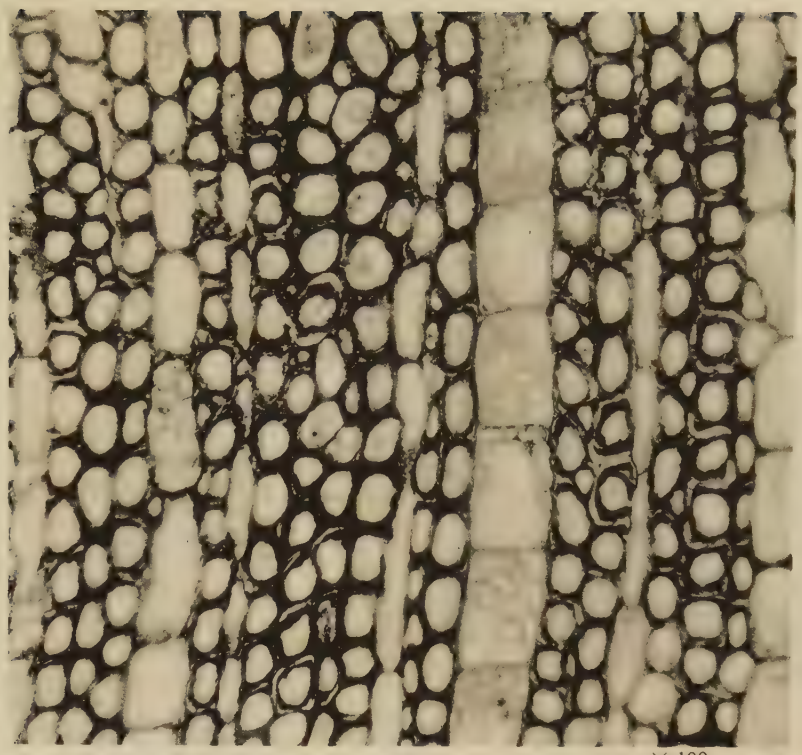
× 90+. 6



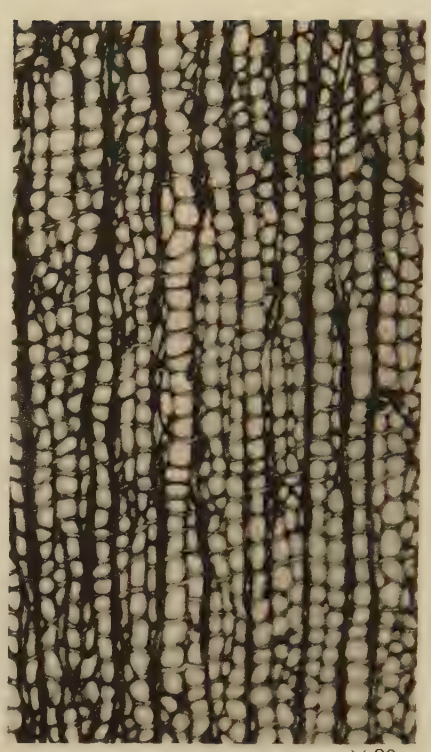
× 90. 5

Cycadeoid Wood Structure.—Continued.

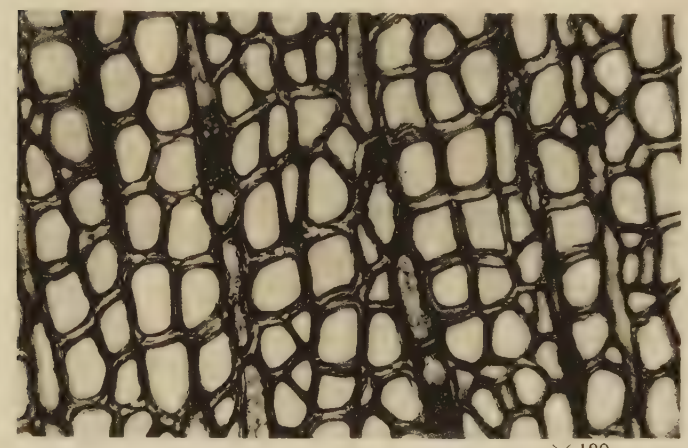
1, 2, Bennettites (=Cycadeoidea) Gibsonianus; 3, 4, 5, Cycadeoidea Paynei; 6, Cycadeoidea Dartoni.



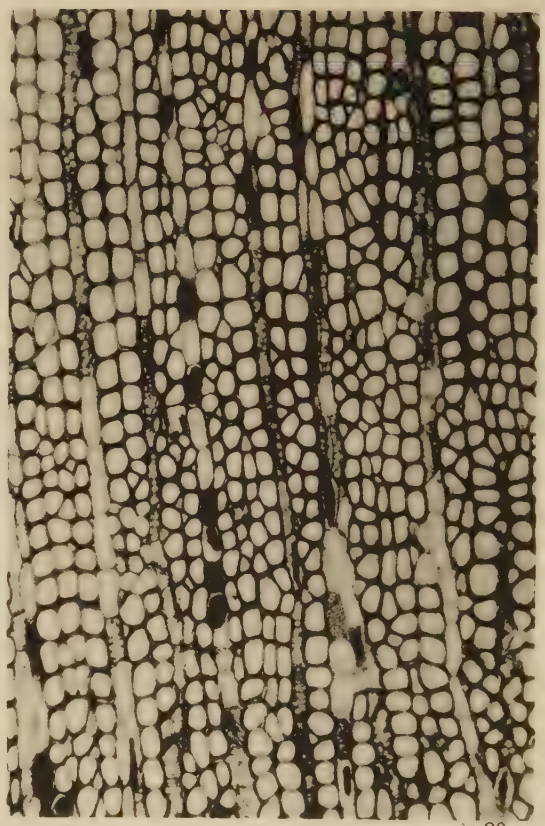
1 × 180.



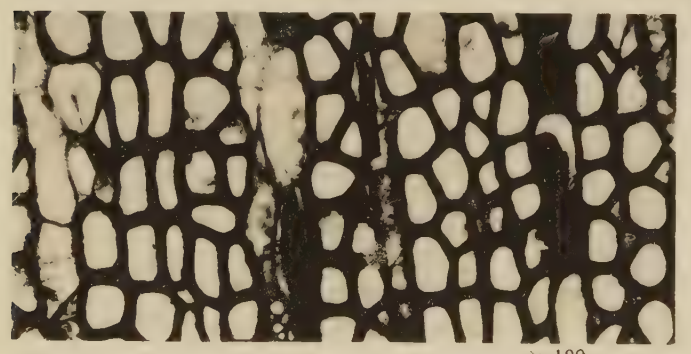
3 × 90.



2 × 180.



4 × 90.



5 × 180.

Cycadeoid Wood Structure—Continued.

1, Bennettites Gibsonianus; 2-3, Cycadeoidea Dartoni; 4, 5, Cycadeoidea Paynei.

Cycadeoidea nana (?). × 0.35.

Lateral Views of Branched Trunk.

Y. T. 210, × 0.3.

Cycadeoidea Dartoni.

Obverse View given on Plate 39.

Y. T. 210, × 0.3.

Cycadeoidea Dartoni.

Obverse Lateral View given on Plate 38.

S. 887, × 1.

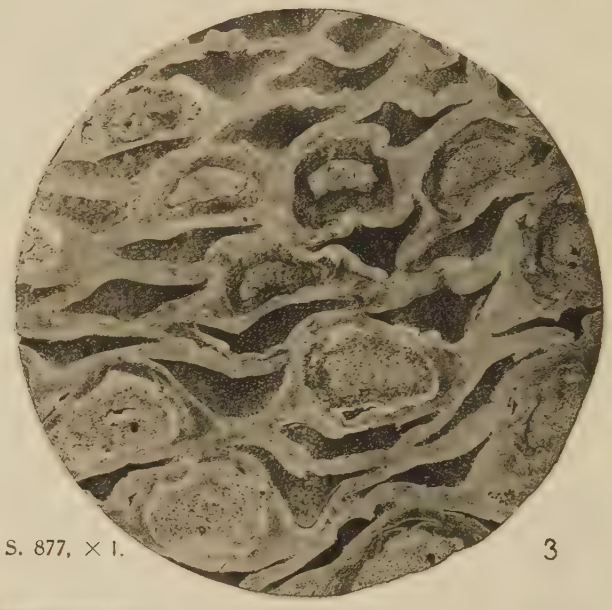
1

S. 878, × 1.

2

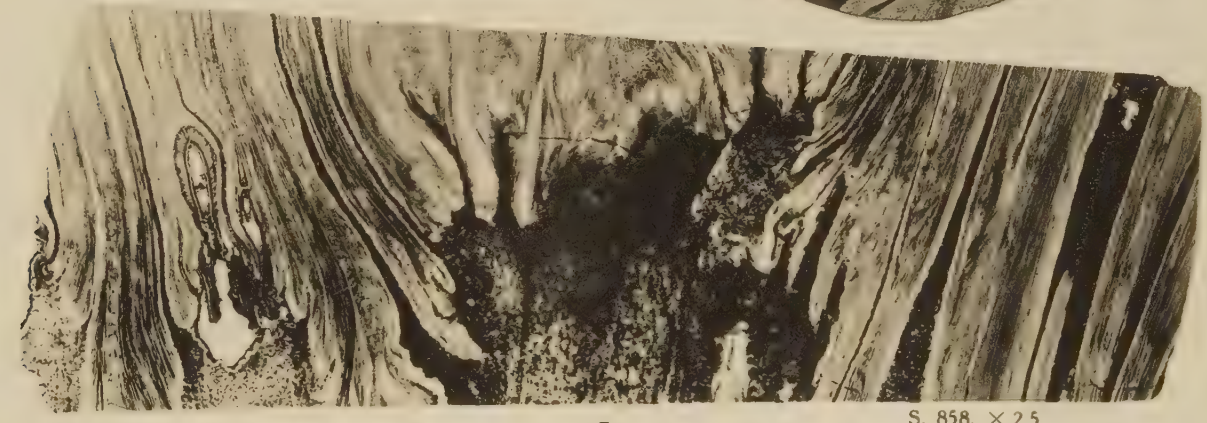
S. 870, × 1.

4



S. 877, × 1.

3



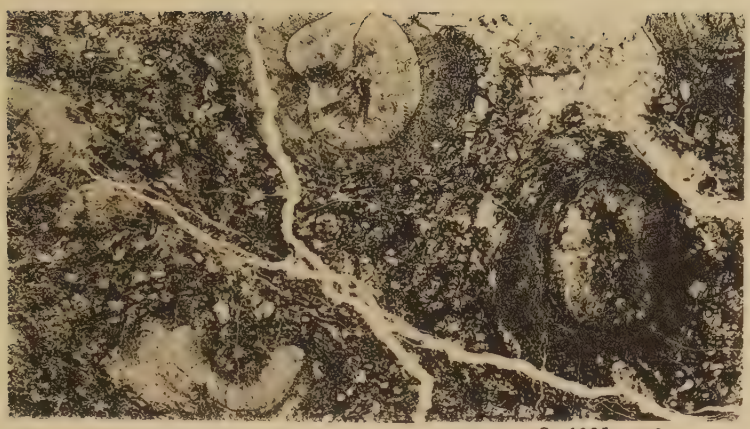
S. 858, × 2.5.

5

Cycadeoidea Dartoni. Y. T. 210.—Continued.

Cycadeoidea Dartoni. ×⅓.

U. S. National Museum Type from Hermosa, South Dakota.

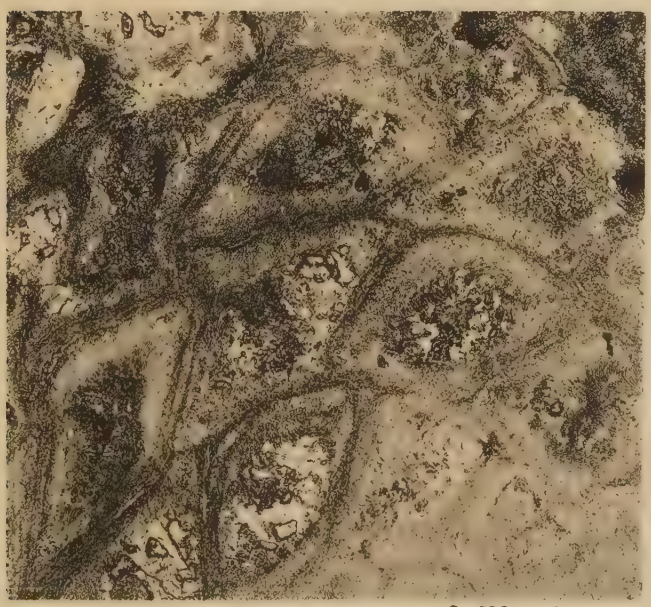


3

S. 1005, ×3.

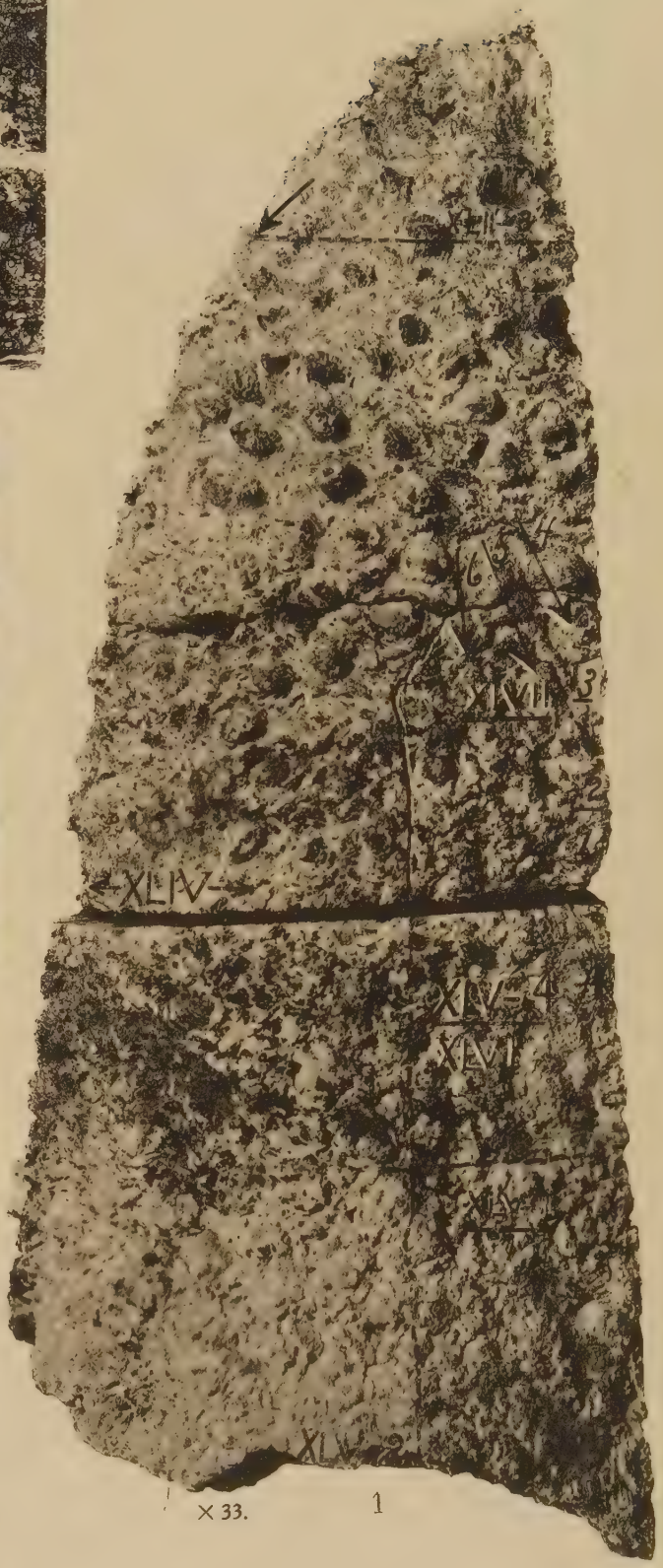
2

S. 100, × 7.



4

S. 895, × 3.



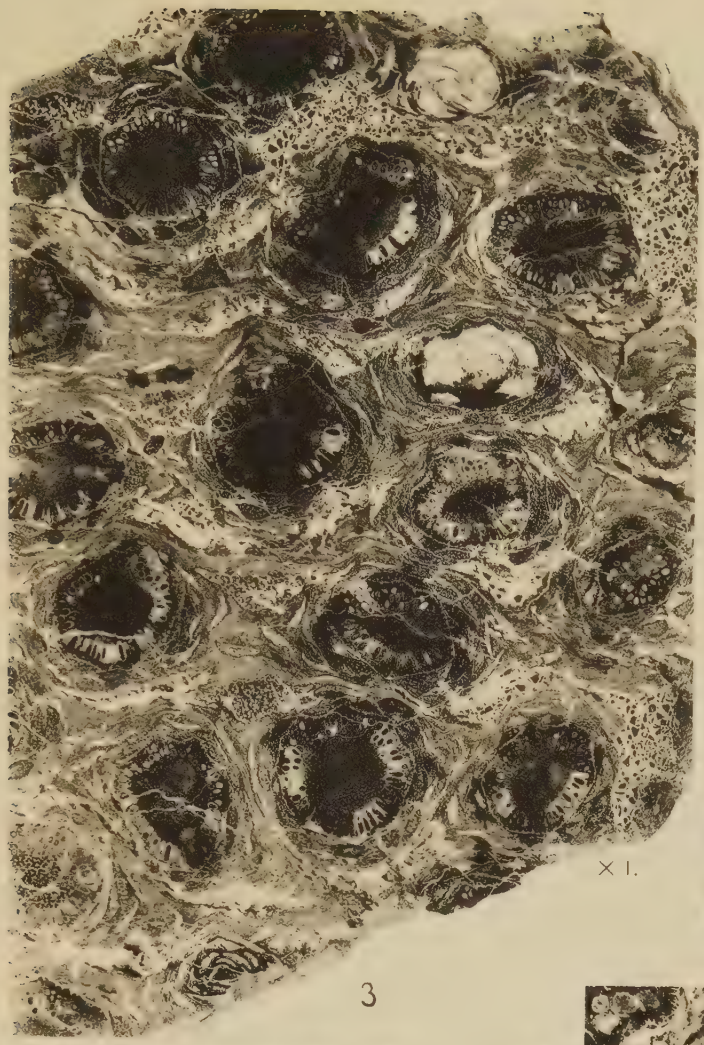
× 33. 1

Cycadeoidea Dartoni (Type)—Continued.

1, Obverse View of Trunk; 2-4, Structure Details.

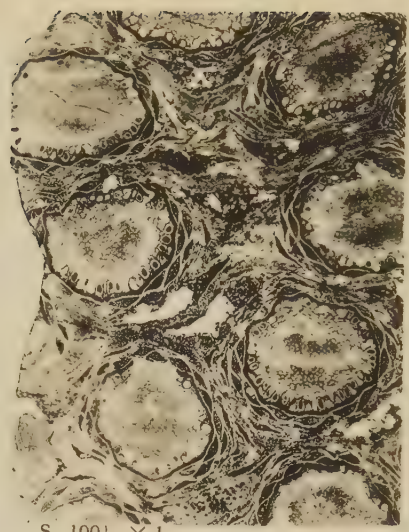
Dartoni (Type). Natural Size.
Longitudinal Section of Trunk Segment.

Cycadeoidea Dartoni (Type). Natural Size.
Transverse Section of Trunk on Saw-cut Line of Plate 43.



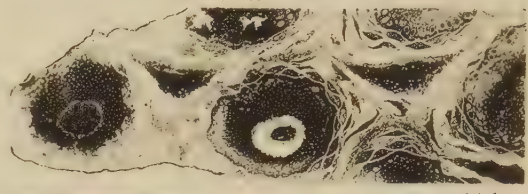
× 1.

3



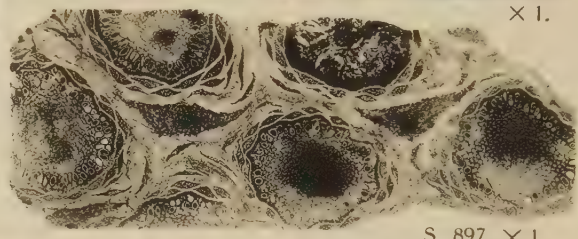
S. 1001. × 1.

4



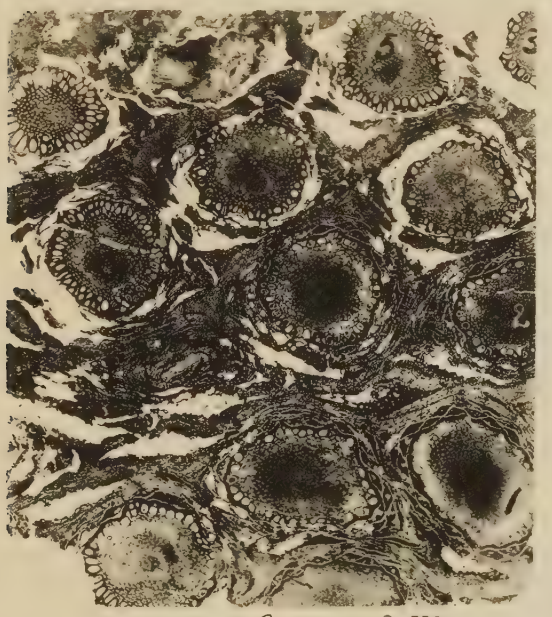
× 1.

2



S. 897. × 1.

1



6 S. 999. × 1.

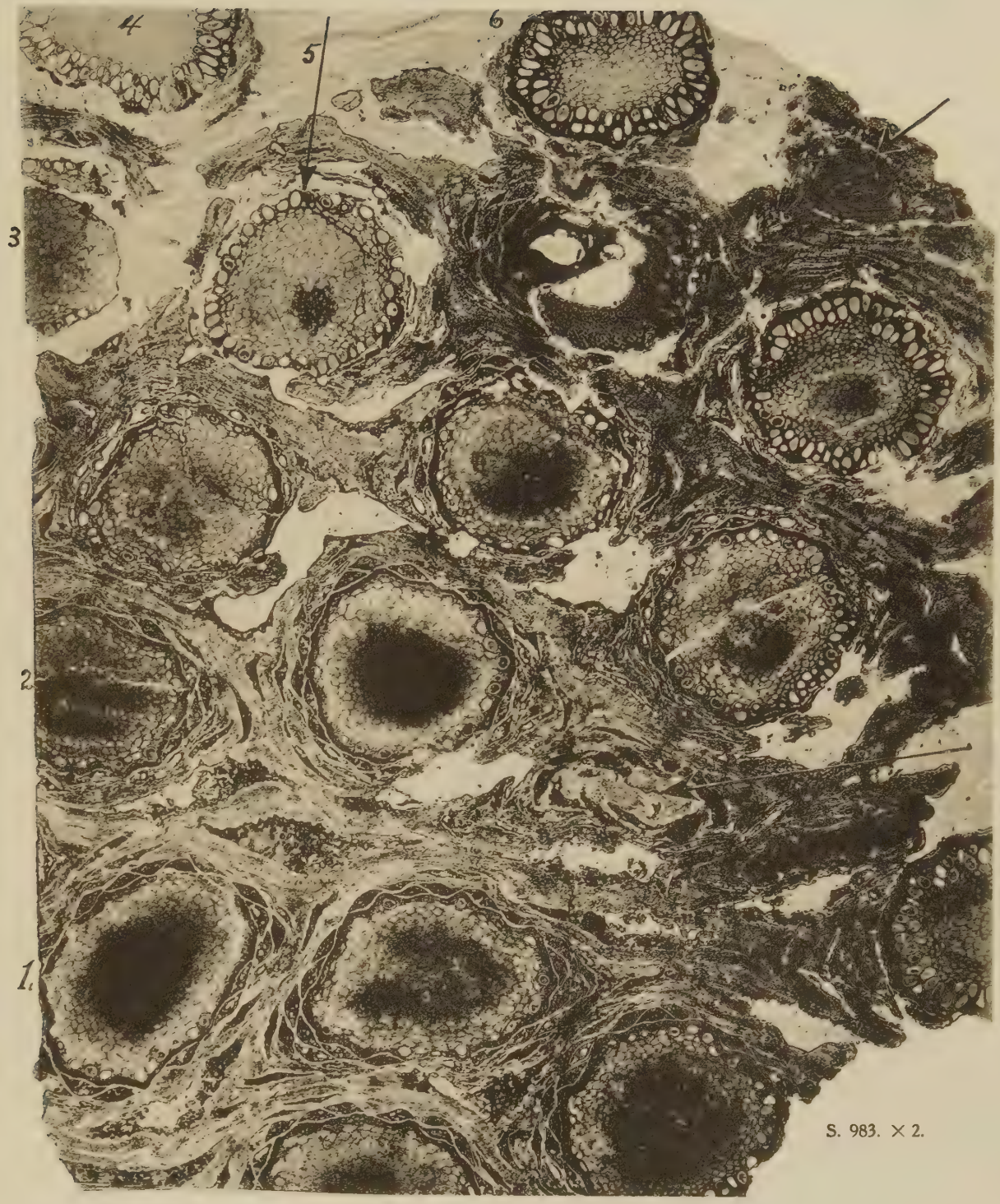
5 × 3.

Cycadeoidea Dartoni. (Type) — Continued.

Series of Transverse Armor Sections.

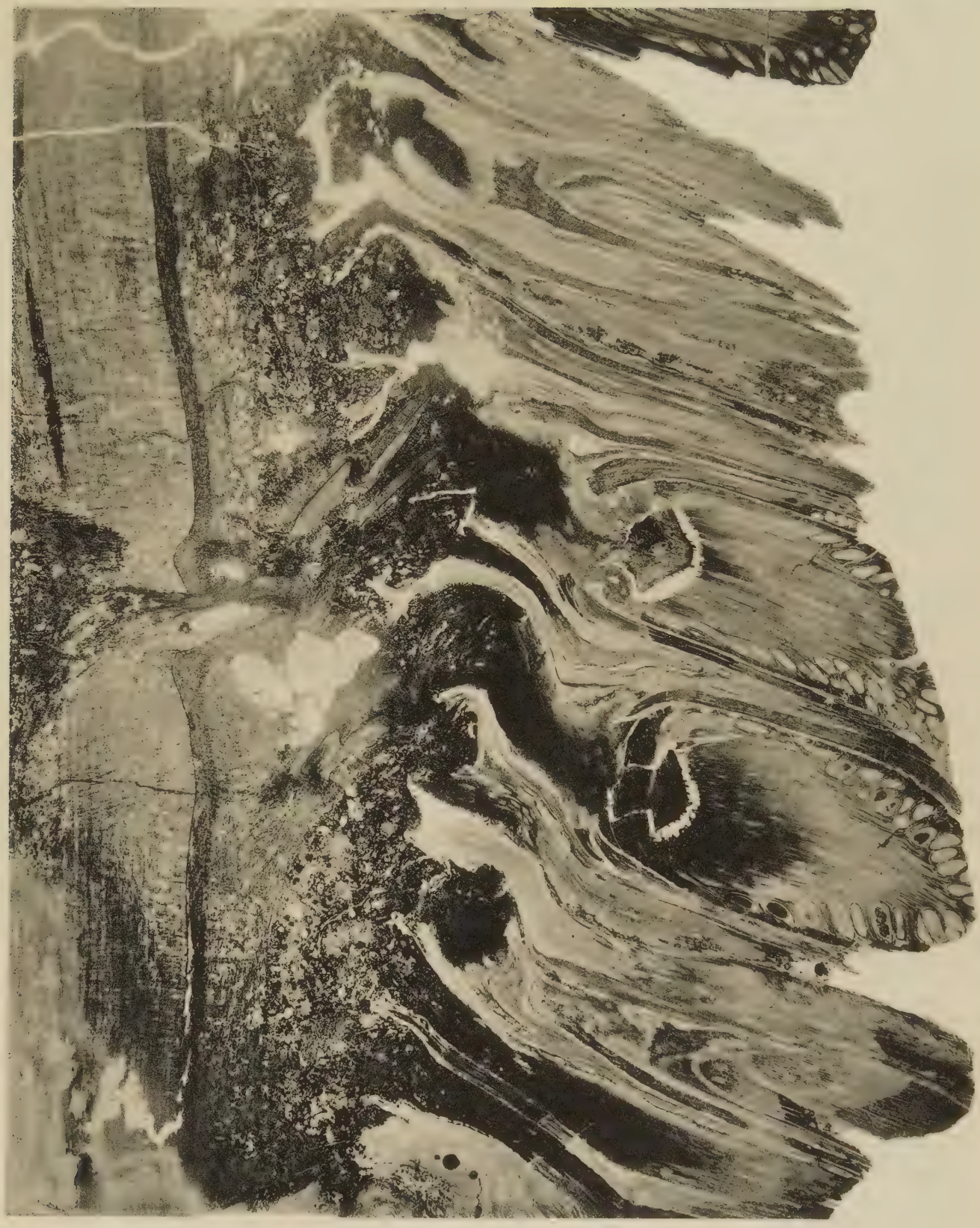
S. 1001, × 3.

Cycadeoidea Dartoni (Type).—Continued.



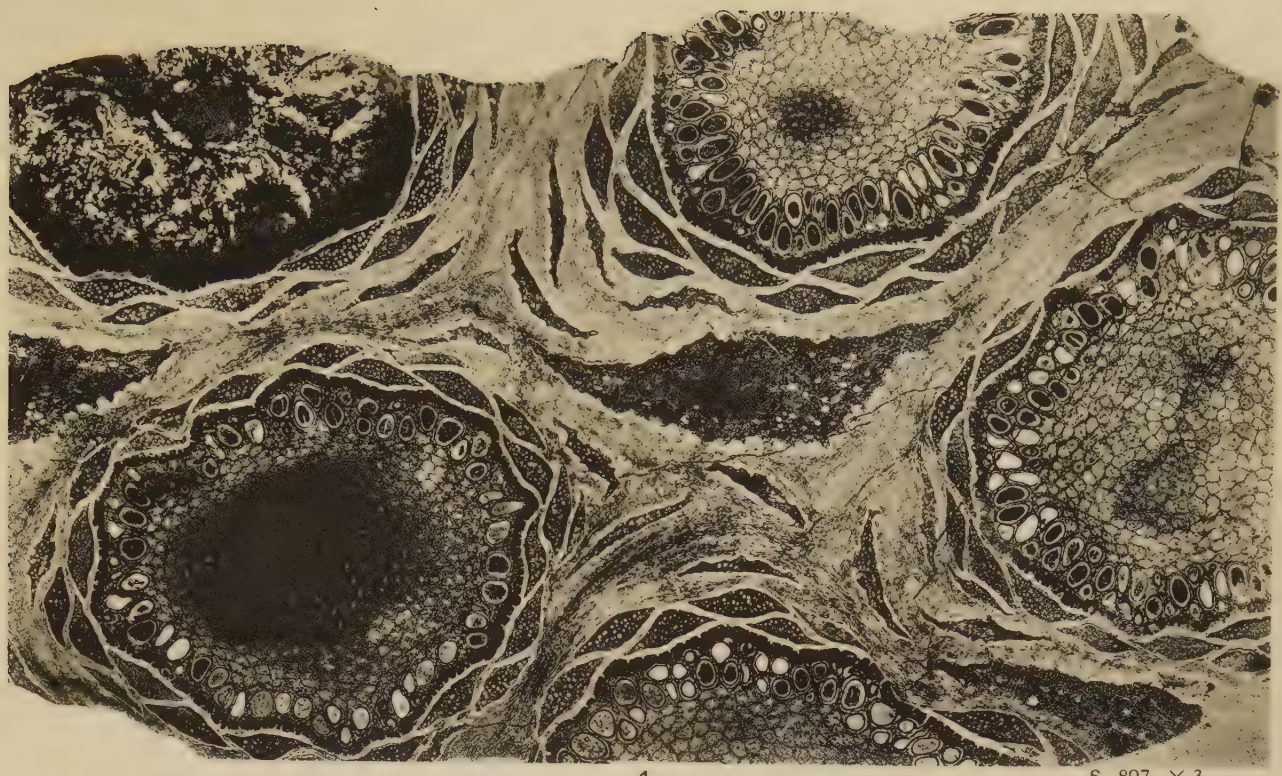
Cycadeoidea Dartoni (Type).—Continued.

For Position of these Cones on Trunk compare notation with that of Figure 1, Plate 42.

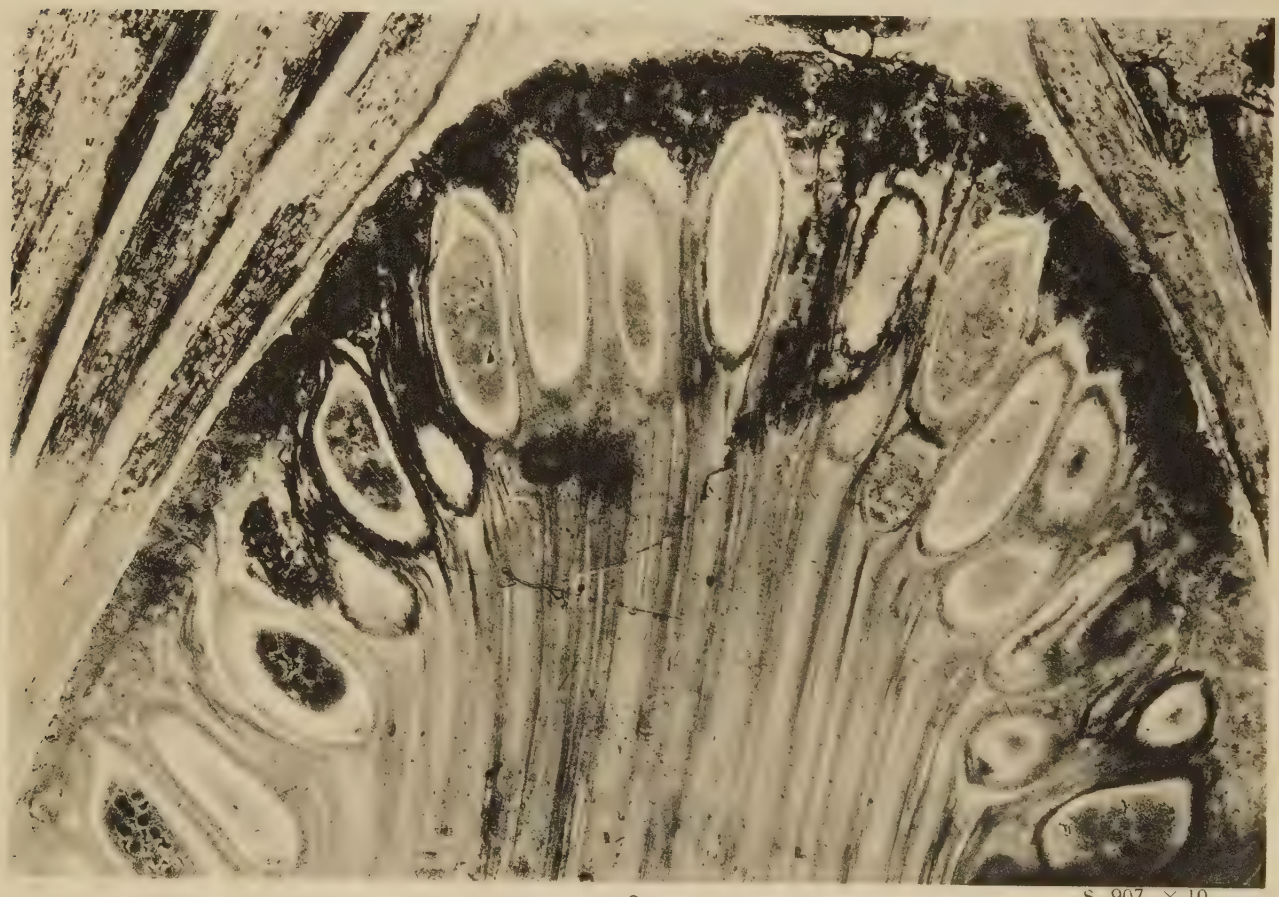


Cycadeoidea Dartoni (Type).—Continued.

Radial Longitudinal Section through Armor, Cortex, and Wood Zone.

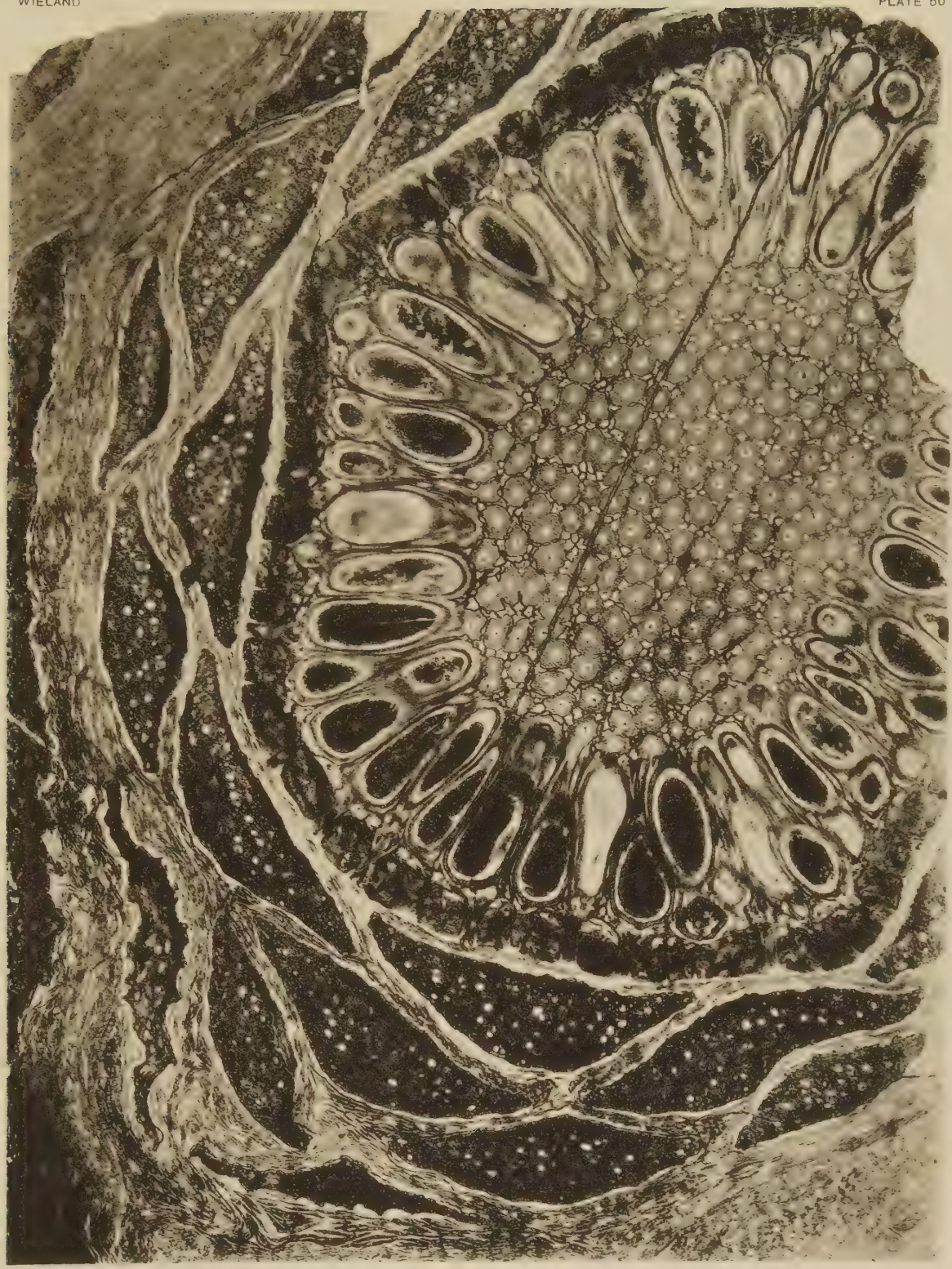


1 S. 897. × 3.



2 S. 907. × 10.

Cycadeoidea Dartoni (Type).—Continued.



S. 917. × 10.

Cycadeoidea Dartoni (Type). Continued.

Y. T. 131, S. 416. ×10.

Cycadeoidea Wielandi (?).

Partly Tangential Section of Strobilus, revealing Surface Characters on Left.

1

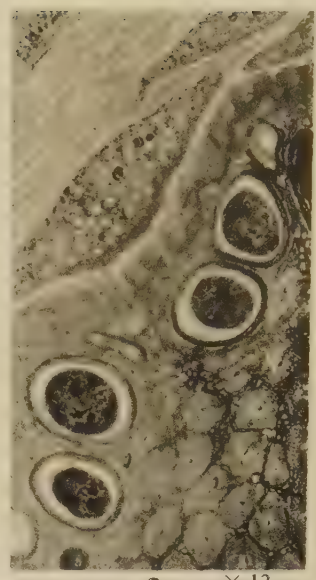
Y. T. 131, S. 909. × 3.

2

Y. T. 210, S. 887. × 3.

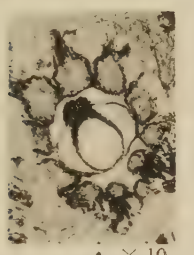
1, Cycadeoidea Wielandi (?); 2, Cycadeoidea Dartoni (?)

1 S. 897, × 40.

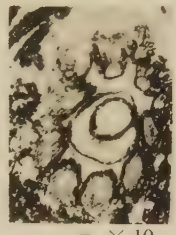


2 × 12.

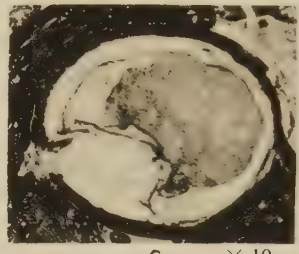
T. 481. 3 × 10.



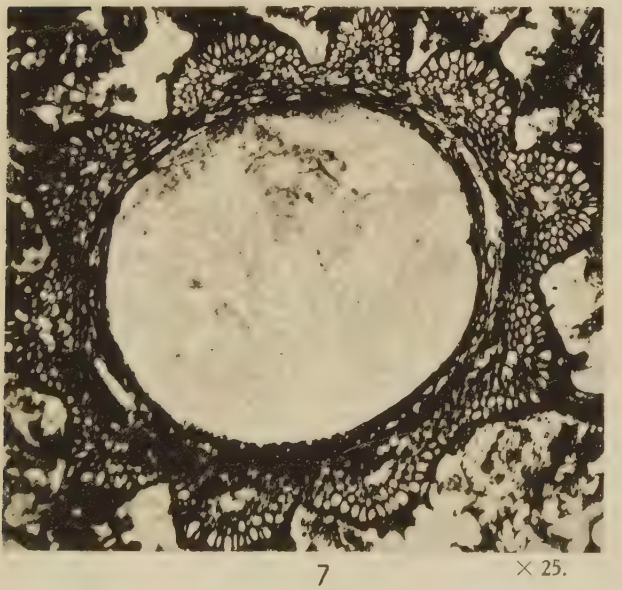
4 × 10.



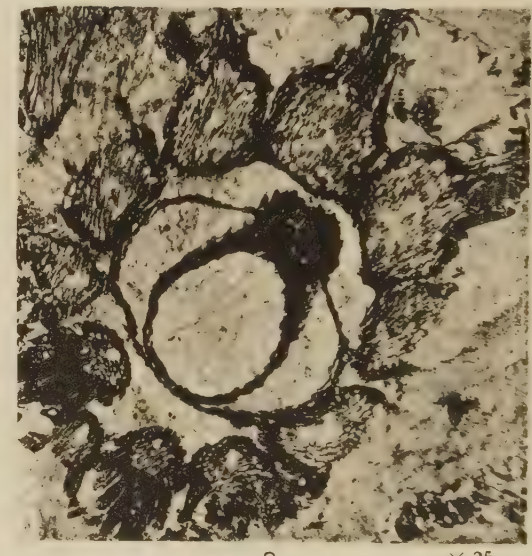
5 × 10.



6 × 10.



7 × 25.

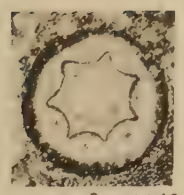


8 × 25.

Cycadeoid and "Coal Ball" Seeds.

1, 2, 3, Cycadeoidea; 6, Lagenostoma; 4, 5, 7, 8, Physostoma.

1 × 40.



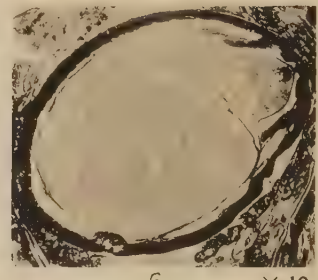
3 × 10.

4 × 10.

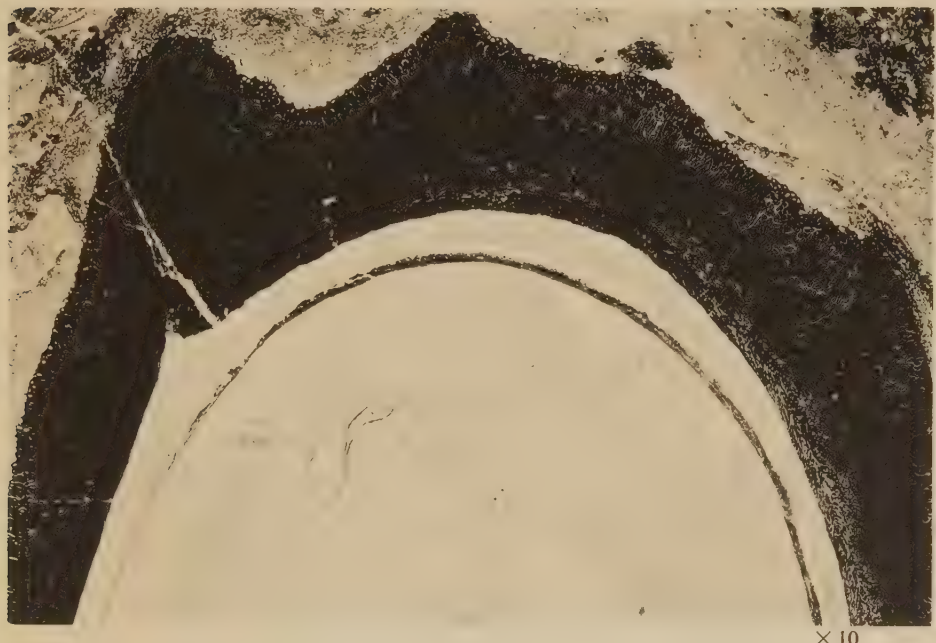
8 × 10.

5 × 10.

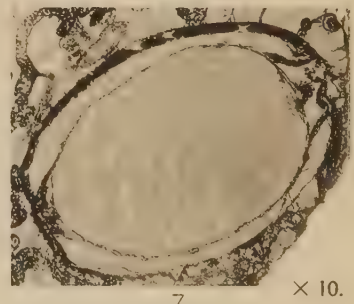
9 × 10.



6 × 10.



2 × 10.



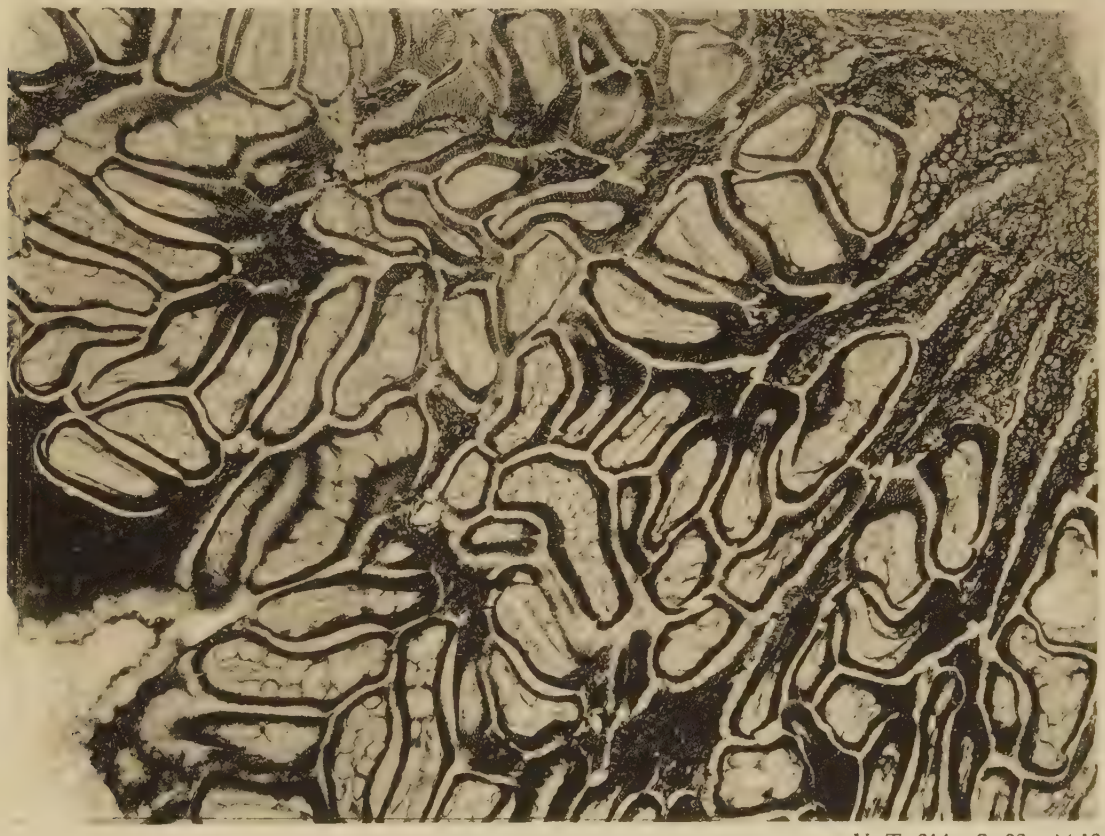
7 × 10.

"Coal Ball" Seeds.

1, 3-7, 9, Lagenostoma ovoides; 8, Conostoma oblongum; 2, Trigonocarpus Parkinsoni.

1

× 36.



2

Y. T. 214. S. 82. × 12.

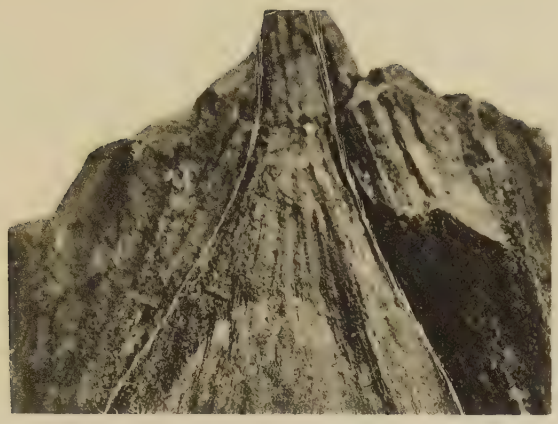
Cycadeoidea dacotensis.

Grouping, Attachment, and Structure of Synangia.

× 16.

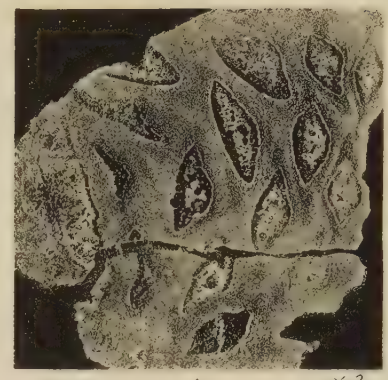
Cycadeoidea dacotensis.

Radical Section through Amphisporangiate Flower-Bud.

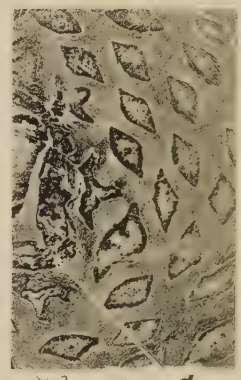


1 × 3.

3 S. 876, × 3.



4 × 3.



× 3. 5 *d*

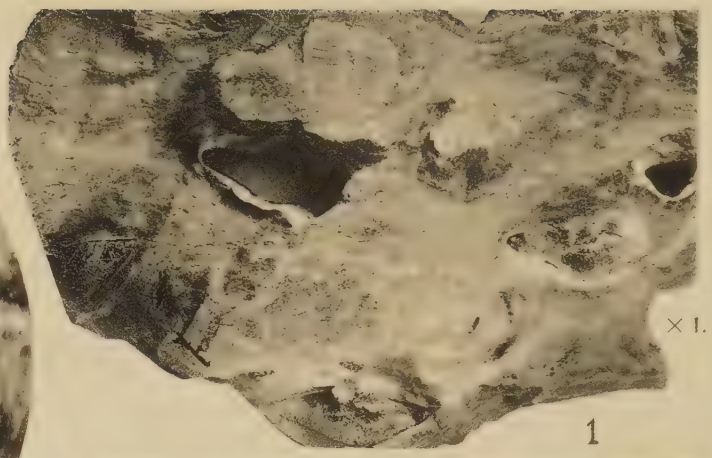
2 S. 880, × 3.

S. 882, × 3.

6

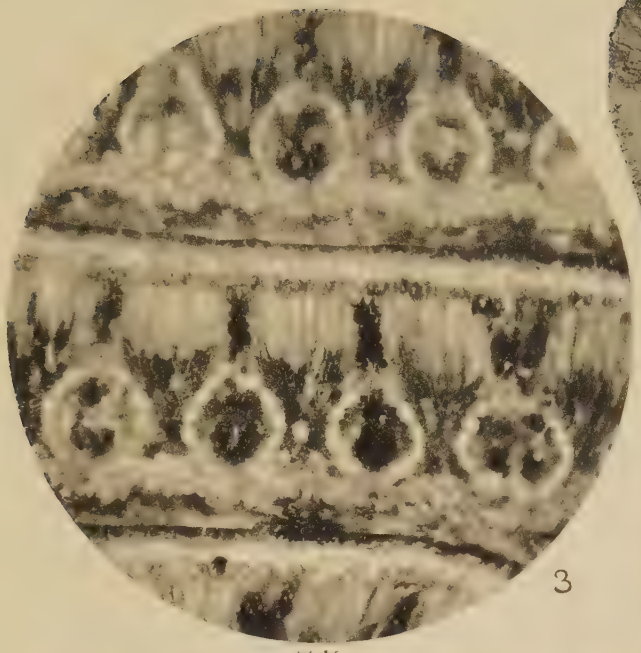
Cycadeoidea Colossalis (?).

Amphisporangiate Flower-Bud: 1, Terminal Dome; 2, Longitudinal, and 3-6, Transverse Sections.



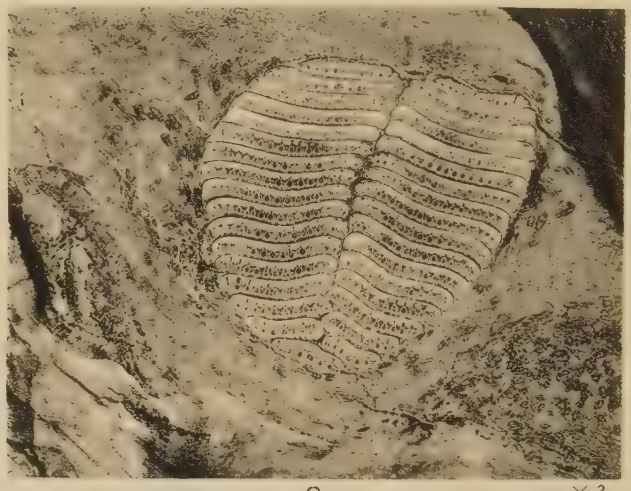
× 1.

1



3

× 16.



2

× 3.

4

× 16.

Y. T. 208, × 3.

5

Cycadeoidean Foliage.

1-4, C. dacotensis (?) ; 5, C. ingens

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